

**Assessing the performance and capture efficiency of the Fukui trap as a removal
tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland,
Canada**

By © Jonathan Andrew Bergshoeff

A Thesis submitted to the School of Graduate Studies in partial fulfillment of the
requirements for the degree of

Master of Science in Marine Biology from the Department of Ocean Sciences

Memorial University of Newfoundland

October 2018

St. John's, Newfoundland and Labrador

Abstract:

Invasive species are recognized as a serious threat to biodiversity, ecosystem functions, plant and animal health, and economic activities. Habitats around the world have been transformed through the negative ecological impacts of invasive species, such as the displacement of native species and changes to community structure. The European green crab (*Carcinus maenas*) is a destructive marine invasive species that can cause widespread damage to invaded ecosystems, and is renowned for its aggression, broad environmental tolerances, and voracious diet. Discovered in Newfoundland waters in 2007, the green crab has since become established in nearshore ecosystems on the south and west coast of the island. Targeted fishing efforts aimed at removing green crabs commonly use Fukui multi-species marine traps, but prior to this thesis the direct interactions between green crabs and these traps had not been formally assessed.

In this study, underwater cameras were used to directly observe Fukui traps as they fished for green crabs. Analysis of these videos revealed that only 16% of green crabs that attempted to enter the Fukui trap were successfully captured. Based on these findings, four distinct trap modifications were designed to increase the number of green crabs caught in Fukui traps per deployment. *In situ* testing of these modifications revealed increased green crab catch-per-unit-effort (CPUE) by as much as 81%, without increasing the impact on non-target species. This thesis demonstrates that modifications to Fukui traps can increase CPUE, thereby making them more effective tools for removing green crabs from invaded ecosystems.

Acknowledgments:

I want to begin by expressing my gratitude to my supervisor, Dr. Brett Favaro. I feel incredibly fortunate to have had the opportunity to work with such a supportive, passionate, and insightful mentor over the course of my degree. Brett's vision and expertise, combined with his continued encouragement as I progressed with this research, has had a significant impact on me both academically and personally.

I also want to thank my committee members, Dr. Cynthia McKenzie and Kiley Best for committing their time, resources, and expertise to this project. Their feedback, support, and wealth of green crab knowledge have been invaluable to the development of my research.

I would like to thank the staff at the Marine Institute's Centre for Sustainable Aquatic Resources (CSAR) for providing me with a supportive and welcoming environment to conduct this research. I especially want to thank my labmates Nicci Zargarpour and Phillip Meintzer, for infusing day-to-day life at CSAR with their friendship and encouragement.

This study was supported by the generous involvement of many individuals who contributed to the fieldwork conducted for this research. I want to express a huge thank you to Fisheries and Oceans Canada staff from the Aquatic Invasive Species program, the MUN Field Services dive team, Nicci Zargarpour, and Mary Alliston Butt for helping me to conduct my research.

This project was supported through funding provided by the Marine Environmental Observation Prediction and Response (MEOPAR) Early-Career Faculty

Development Grant awarded to Dr. Brett Favaro et al. (EC1-BF-MUN), and by an Ocean Industry Student Research Award from the Research and Development Corporation of Newfoundland and Labrador (5404-1915-101). In-kind support was provided by Fisheries and Oceans Canada in the form of staff time, bait, and Fukui traps.

Finally, I would like to express my gratitude to my family for their support. Deepest thanks to my wife Rebecca, who has supported me throughout this process with unwavering love and encouragement.

Table of Contents:

Abstract:	ii
Acknowledgments:	iii
Table of Contents:	v
List of Tables:	vi
List of Figures:	vii
Chapter 1: General Introduction	1
Co-authorship Statement:.....	12
Chapter 2: Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (<i>Carcinus maenas</i>) in Newfoundland, Canada.....	13
Chapter 3: Improving the efficiency of the Fukui trap as a capture tool for the invasive European green crab (<i>Carcinus maenas</i>) in Newfoundland, Canada	61
Chapter 4: Summary	95
References:.....	102

List of Tables:

Chapter 2:

Table 2.1. Summary of green crabs caught at each study site in 2015.47

Table 2.2. Summary of all bycatch species caught at each study site in 2015.48

Table 2.3. Summary of data from each video that was analyzed.49

Chapter 3:

Table 3.1. Summary of trap deployments at Fox Harbour, NL and North Harbour, NL. .83

Table 3.2. Summary of all bycatch species captured in each trap type.84

Table 3.3. Summary of green crab captured in each trap type.85

Table 3.4. Estimated regression parameters, standard errors, z-values, and P-values for the negative binomial generalized linear mixed-effects model (GLMM) presented in Eqn (1).86

Table 3.5. Estimated regression parameters, standard errors, t-values, and P-values for the linear mixed-effects model (LME) presented in Eqn (2).87

List of Figures:

Chapter 1:

Figure 1.1. Image of a standard Fukui trap showing dimensions and entry-slit location (dotted white lines) (A), and a Fukui trap deployed to fish for green crabs (B).....	11
--	----

Chapter 2:

Figure 2.1. A visual representation of the six steps required for a green crab to be captured.....	50
Figure 2.2. The camera frame constructed around a Fukui trap and its field of view.	51
Figure 2.3. Map of 2015 and 2016 study sites across Newfoundland.	52
Figure 2.4. Plots comparing green crab catch and fishing duration between Fair Haven, NL and Little Port Harmon, NL.....	53
Figure 2.5. A screen shot from a video recording showing the top-down view of a Fukui trap as it actively fishes in situ.	54
Figure 2.6. Green crab accumulation over the course of each trap deployment (n = 8)....	55
Figure 2.7. The proportional outcome and average time taken for all green crab entry attempts into the Fukui trap.	57
Supplementary Figure 2.1. Video selection key used to determine which videos were suitable for analysis.....	58

Chapter 3:

Figure 3.1. The four different trap modifications: sinker (A), mesh (B), assist (C), string (D).	89
Figure 3.2. Maps showing the location of our study sites and experimental blocks.	90
Figure 3.3. Boxplot illustrating the average number of green crabs captured in each trap type.....	91
Figure 3.4. A boxplot illustrating the average carapace width of green crabs captured in each trap type.	92
Supplementary Figure 3.1. A boxplot illustrating the average number of green crabs captured at each block.....	93

Chapter 1: General Introduction

Invasive species are taxa that have become established in an area outside of their historic range and that have the capacity to harm ecosystems, human health, biodiversity, and the economy (Lowe et al., 2000; Bax et al., 2003; Lodge et al., 2006; Beck et al., 2008). Invasive species are recognized as a serious threat to biodiversity, and in many cases can cause a range of ecological impacts on invaded ecosystems, from predation-mediated extinctions of native prey, to shifts in the distribution and abundance of native species through competition for habitat and resources (Gurevitch & Padilla, 2004; Molnar et al., 2008; Butchart et al., 2010). In the marine environment, few invaders are more notorious than the European green crab (*Carcinus maenas*) (Linnaeus, 1758) (EPA, 2008; Jeffery et al., 2017). This invasive crustacean has been ranked among 100 of the world's 'worst invasive alien species' by the International Union for Conservation of Nature, and is recognized as a highly destructive predator in nearshore coastal communities (Lowe et al., 2000; Leignel et al., 2014).

Originating in the coastal and estuarine waters of Europe and North Africa, the European green crab (hereafter, green crab) has a long history of range expansion (Le Roux, Branch & Joska, 1990; Grosholz & Ruiz, 1995, 1996; Walton et al., 2002; Carlton & Cohen, 2003; Hidalgo, Barón & Orensanz, 2005; Therriault et al., 2008). To date, green crabs have spread to every continent around the world with temperate shores, including North and South America, South Africa, Australia, and Asia (Furota et al., 1999; Thresher et al., 2003; Robinson, Griffiths & Kruger, 2004; Hidalgo, Barón &

Orensanz, 2005; Klassen & Locke, 2007; Behrens Yamada & Gillespie, 2008; Darling et al., 2008; Blakeslee et al., 2010).

In North America, the green crab has established invasive populations on both the Pacific and Atlantic coasts. On the west coast, the invasion began in San Francisco Bay, California in 1989 (Cohen, Carlton & Fountain, 1995; Grosholz & Ruiz, 1995; Therriault et al., 2008). Current green crab distributions on the Pacific coast have expanded from California, USA (Cohen, Carlton & Fountain, 1995; Grosholz & Ruiz, 1995) up to Central Coast of British Columbia, Canada (Behrens Yamada et al., 2005; Gillespie et al., 2007, 2015; Behrens Yamada & Kosro, 2010; Duncombe & Therriault, 2017). On the east coast, the green crab invasion dates back to the early nineteenth century, when they were first observed in Massachusetts in 1817 (Say, 1817). Over the next 100 years, green crabs spread northward into Canadian waters, where they were first observed in Passamaquoddy Bay, New Brunswick and subsequently spread throughout the Bay of Fundy (Leim, 1951; MacPhail, 1953; Hart, 1955). During the 1990's, green crab populations became established in Nova Scotia and eventually spread throughout the Canadian Maritimes (Carlton & Cohen, 2003; Klassen & Locke, 2007; Blakeslee et al., 2010). Eventually, green crabs arrived in the coastal waters of Newfoundland in 2007, when both juvenile and adult green crabs were reported in North Harbour, Placentia Bay (DFO, 2011a; McKenzie et al., 2011). Current green crab distributions on the Atlantic coast range from Virginia, USA to Newfoundland, Canada (Jeffery et al., 2017).

Genetic evidence suggests that green crab populations on the Atlantic coast originated from two distinct introduction events, contributing to both a southern and

northern genotype with differing environmental tolerances (Jeffery et al., 2018; Lehnert et al., 2018). First, the historical invasion of Maine, USA in the early 1800's by green crabs originating from the southern United Kingdom (Say, 1817; Roman, 2006; Blakeslee et al., 2010). Second, an introduction into north-eastern Nova Scotia, Canada in the late 1980's by green crabs originating from the northern limit of its range in Europe (Roman, 2006). Green crabs originating from the second introduction event were more cold-tolerant, allowing them to become established throughout the colder regions of the Canadian Maritimes, and eventually spreading to Newfoundland (Roman, 2006; Blakeslee et al., 2010). Genetic analysis of Newfoundland green crabs reveals a hybridized population comprised of both the southern and northern genotype (Blakeslee et al., 2010; Jeffery et al., 2017; Lehnert et al., 2018).

As green crabs spread, they have caused large-scale and destructive changes to invaded ecosystems (Lowe et al., 2000; Klassen & Locke, 2007; Rossong et al., 2012). Some of these negative effects include damage to eelgrass (*Zostera marina*) beds through destructive foraging and burrowing behaviours (Klassen & Locke, 2007; Matheson et al., 2016), predation-induced impacts on bivalve populations (Miron et al., 2005; Kimbro et al., 2009; Pickering & Quijón, 2011; Matheson & McKenzie, 2014), and aggressive competition with native species for food and habitat (Le Roux, Branch & Joska, 1990; Cohen, Carlton & Fountain, 1995; Rossong et al., 2006, 2012). The impacts of green crabs on eelgrass are especially concerning because eelgrass beds are critical nearshore habitat for species such as Atlantic cod (*Gadus morhua*) and American lobster (*Homarus*

americanus), and therefore, pose both an ecological and economic threat (Joseph, Schmidt & Gregory, 2013; Matheson et al., 2016).

The impacts of green crabs on invaded ecosystems are further compounded by the fact that they are voracious generalists that predate upon many organisms (e.g., gastropods, bivalves, polychaetes, and crustaceans) (Ropes, 1968; Grosholz & Ruiz, 1996; Hidalgo et al., 2007; Leignel et al., 2014; Matheson & McKenzie, 2014), have rapid growth and high fecundity which allows them to quickly disperse and establish new populations (Behrens Yamada, 2001; Hänfling, Edwards & Gherardi, 2011; Leignel et al., 2014), and can tolerate wide ranges in salinity, oxygen, and temperature (Broekhuysen, 1936; Crothers J. H., 1968; Eriksson & Edlund, 1977; Cohen, Carlton & Fountain, 1995). Such traits make green crabs extremely adaptable and an ideal global invader that poses a serious threat to invaded marine ecosystems (Carlton & Cohen, 2003; Roman & Palumbi, 2004; Darling et al., 2008; Blakeslee et al., 2015).

The complete eradication of an aquatic invasive species such as the green crab is virtually impossible once the organism has become established in an invaded ecosystem (Bax et al., 2003; Thresher & Kuris, 2004; Lodge et al., 2006), and may only be possible if the invasion is in a confined area and is addressed shortly after arrival (Culver & M. Kuris, 2000; Simberloff, 2001; Bax et al., 2002). Furthermore, removal efforts aimed at controlling invasive species are logistically challenging and resource intensive (Myers et al., 2000; Taylor & Hastings, 2004; Lodge et al., 2006; Coutts & Forrest, 2007).

Therefore, modern marine invasion science and a growing body of research is focused on estimating targets for invasive species removal, with the goal of reducing the density of

invasive species to a point that promotes the protection of native species and the maintenance of ecosystem structure and function (Perrings, 2005; Green et al., 2014). If the population of an invasive species can be suppressed below a certain threshold, the native ecosystem can still function despite the presence of the invader, even if complete eradication is impossible (Green et al., 2014). This has been demonstrated with invasive Indo-Pacific lionfish (*Pterois volitans* and *Pterois miles*) in the Bahamas, where reducing the populations of lionfish to specific densities protected native fish community biomass from predation-induced declines (Green et al., 2014). In this study, Green et al. (2014) developed a model to predict reef-specific lionfish densities beyond which native fishes would decline due to predation. Depending on the reef, Green et al. found that reductions in lionfish density of 25-92% were sufficient to prevent lionfish from overconsuming native prey, and that if lionfish were kept below these densities then native fish biomass increased by 50-70%. Therefore, this study demonstrated that for ongoing invasions, reductions in the density of an invasive species can limit ecological harm and protect the ecosystem on a local scale, even when complete eradication of the invader is impossible.

Reducing the density of an invasive species requires the establishment of a removal program, which can involve biological control, chemical control, genetic modification, or physical removal (Bax et al., 2003; Secord, 2003; Thresher & Kuris, 2004). In the marine environment, control measures for mobile invaders often consist of physical removal through targeted fishing (Thresher et al., 2000; Thresher & Kuris, 2004; Green et al., 2014). Therefore, the effectiveness of these physical removal efforts will be influenced by the efficiency of the gear being used (Vazquez Archdale et al., 2003;

Vazquez Archdale, Anasco & Nakagawa, 2010; Bergshoeff et al., 2018). Currently, there are no specific removal targets for green crabs based on threshold densities. However, regardless of what these removal targets may be, it is important to establish an effective removal program. In doing so, it is possible that ecological benefits similar to those observed in the lionfish study by Green et al. (2014) can be achieved through targeted fishing in ecosystems invaded by green crabs. To achieve these results, removal effort using the Fukui trap need to be as efficient as possible to promote the highest possible catch-per-unit effort (CPUE). A better knowledge of CPUE with the Fukui trap would aid in establishing removal targets for green crabs and is critical for designing efficient mitigation and management plans.

Following the discovery of green crabs in the coastal waters of Newfoundland in 2007, a pilot project was developed by Fisheries and Oceans Canada (hereafter, DFO) to confirm and assess the status of the green crab invasion. This pilot project was followed by a more detailed ecological assessment and research in subsequent years (DFO, 2011a,b). The complete eradication of green crabs was not considered an option; therefore, it was concluded that focused trapping would be the most effective management strategy to suppress invasive populations to slow their spread and minimize their negative effects on the native ecosystem. The direct removal of green crabs through intensive trapping has become the current method of conducting targeted removals of green crabs on both the east and west coast of Canada (DFO, 2011b,a; Duncombe & Therriault, 2017). This targeted and intensive trapping has proven to be an effective method of reducing green crab populations in invaded areas and has been shown to limit

their negative impacts on invaded ecosystems. Furthermore, in some systems it has been shown that consistent trapping gradually decreases the average body size of green crab populations, promoting a shift in their ecological role from primary predators to potential prey for native species (e.g., shorebirds and native crustaceans) (DFO, 2011a). Finally, changes in population structure and demographics can have implications on reproductive output, with reductions in body size and age contributing to reductions in the reproductive capacity of a green crab population (Duncombe & Therriault, 2017).

A variety of fishing gears can be used to capture green crabs, including whelk pots (DFO, 2011b), eel traps (Cameron & Metaxas, 2005; Vercaemer & Sephton, 2016), fyke nets (Poirier et al., 2018), shrimp traps (Vercaemer & Sephton, 2016), and minnow traps (Gillespie et al., 2007). In Canada, green crab removal efforts often rely on the Fukui multi-species marine trap (model FT-100, Fukui North America, Eganville, Ontario, Canada) to capture green crabs (Behrens Yamada et al., 2005; Rossong et al., 2012; Best, McKenzie & Couturier, 2014, 2017; Duncombe & Therriault, 2017). Trap comparison studies have shown the CPUE of the Fukui trap to be significantly higher than both shrimp and eel traps (Vercaemer & Sephton, 2016). The standard Fukui trap used for capturing green crabs consists of a rectangular, vinyl-coated high tensile steel frame (60 x 45 x 20 cm) covered with square, single-knotted polyethylene mesh (12 mm bar length) (Figure 1.1). There are two entrances at either end of the trap, where two netting panels form a horizontal “V” with a 45 cm expandable entry slit at the narrow end. To enter the trap through either of these entrances, green crabs must force themselves through the entrance, which remains tightly compressed in its default

position. These traps are practical for removal efforts as they are light-weight, collapsible, durable, and can be easily deployed from small boats or from shore.

The long-standing invasion history of the green crab, and its success as an invasive species has prompted extensive research investigating the impacts and ecological consequences of green crabs on invaded ecosystems (Grosholz & Ruiz, 1996; Leignel et al., 2014; Matheson et al., 2016). However, there has been comparatively little research focused on how the Fukui trap can be optimized as a tool for reducing green crab numbers in invaded ecosystems. The Fukui trap has proven to be a satisfactory tool for removing green crabs, and despite its widespread use for research, monitoring, and mitigation, there have been no formal studies of the interactions between green crabs and the standard Fukui trap, and substantial knowledge gaps exist surrounding the overall efficiency of this fishing gear.

The most effective way to understand the interactions between an animal and a piece of fishing gear is through the use of underwater video (Favaro et al., 2012; Underwood, Winger & Legge, 2012). Underwater cameras can be used to better understand a variety of different fishing gears, including hooks (He, 2003; Robbins et al., 2013; Grant, Sullivan & Hedges, 2018), trawls (Nguyen et al., 2014; Underwood et al., 2015), and pots (also referred to as traps) used to target fish (Bacheler et al., 2013a; Favaro, Duff & Côté, 2013; Meintzer, Walsh & Favaro, 2017) and crustaceans (Jury et al., 2001; Barber & Cobb, 2009; Clark et al., 2017). Underwater video is essential to better understanding the Fukui trap as a capture tool for green crabs and is the only way to accurately assess the outcome of each attempt a green crab makes to enter the trap, and

the likelihood that crabs will remain captured until the trap is retrieved. Furthermore, observations made from underwater videos can reveal information that could not be obtained through catch data alone – providing valuable insight into the performance of the Fukui trap, and potential design modifications that could help to improve the overall capture efficiency of green crabs.

This thesis describes research that was conducted over two consecutive field seasons in 2015 and 2016 across coastal Newfoundland. The first field experiment describes a novel investigation of the interactions between green crabs and the standard Fukui trap. In this study, I used stationary underwater video cameras mounted to Fukui traps deployed *in situ* to assess the performance, efficiency, and design of this fishing gear as a tool for capturing green crabs. Multiple camera-equipped traps were deployed across several regions of Newfoundland invaded by the green crab to observe the capture process. Quantitative analysis of the long-duration video recordings allowed for an accurate assessment of the number of green crabs that approached the Fukui trap, the number and outcome of any entry attempts, and the number of green crabs that escaped the trap before it was retrieved. This information was used to gain an accurate understanding of how well the Fukui trap functions as a tool for capturing green crabs. Observations made from the videos revealed inefficiencies and potential trap improvements that were instrumental in developing a baseline understanding of Fukui trap performance.

The second field experiment was based on my video observations from the 2015 field season. The primary objective of this experiment was to improve the efficiency of

the Fukui trap through simple design modifications. I developed four distinct modifications designed to facilitate the successful capture of green crabs. I tested these modified Fukui traps *in situ* at two locations in Placentia Bay, Newfoundland and compared CPUE between each modified Fukui trap and the standard Fukui trap. The trap modifications were designed to be simple and practical, so that they could be easily applied to existing Fukui traps that are already in use for green crab removal efforts.

The overall goal of the research described in this thesis was to gain a thorough understanding of the performance of the Fukui trap as a capture tool for invasive green crabs, in addition to improving its efficiency through modifications. The Fukui trap is an essential tool for reducing green crab abundance in invaded marine ecosystems, and the versatility of this trap has contributed to its widespread use for green crab removal efforts on both the east and west coasts of North America. Ultimately, a more efficient Fukui trap can help to control green crab populations, reduce abundance in invaded ecosystems, and assist in preserving the function and integrity of these ecosystems.

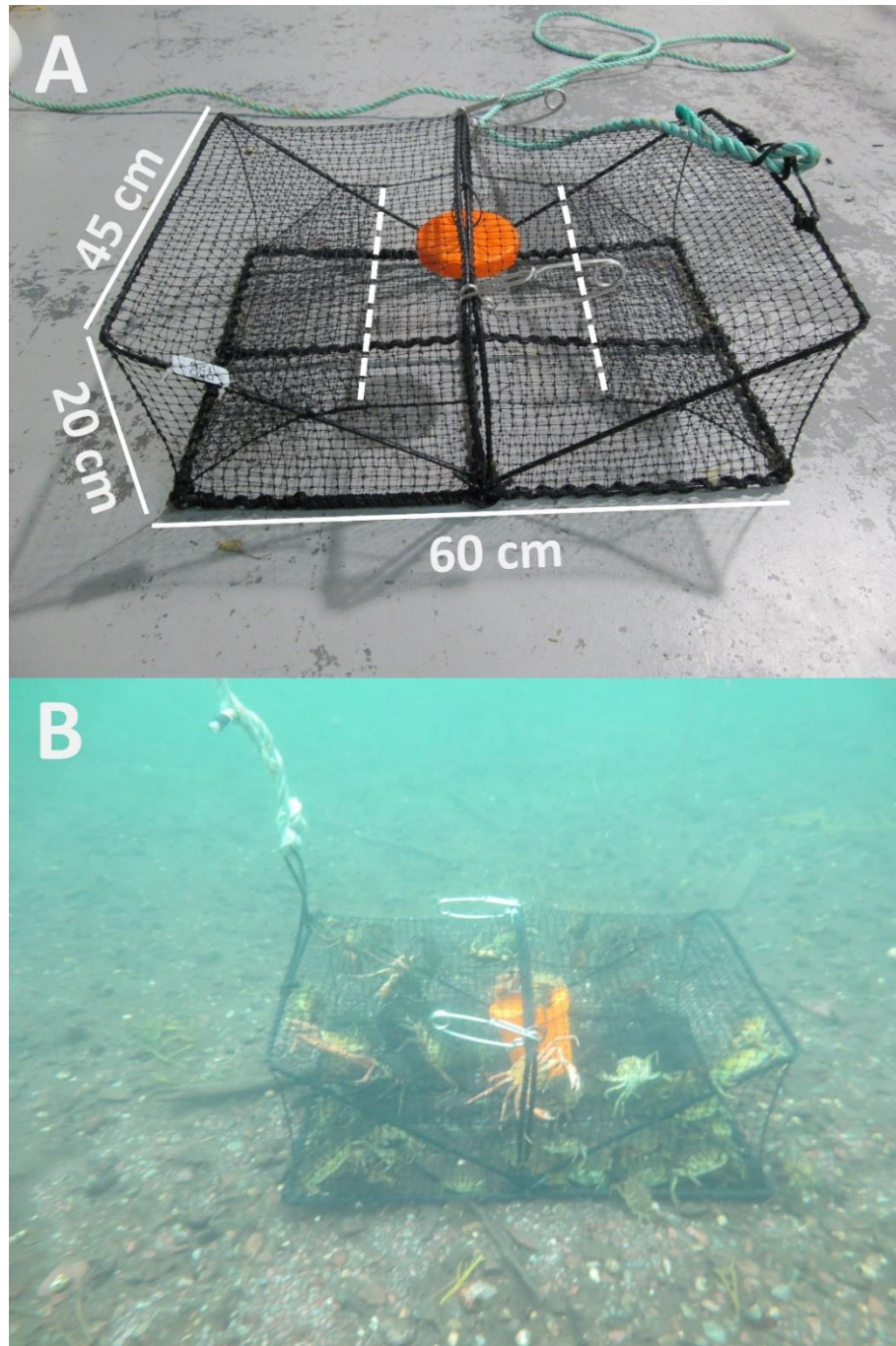


Figure 1.1. Image of a standard Fukui trap showing dimensions and entry-slit location (dotted white lines) (A), and a Fukui trap deployed to fish for green crabs (B).

Co-authorship Statement:

I, Jonathan Bergshoeff, Dr. Cynthia McKenzie, Kiley Best, Nicola Zargarpour, and Dr. Brett Favaro are listed as co-authors on chapter 2 within this thesis, which was submitted for publication. Author contributions for this chapter are as follows. I, Jonathan Bergshoeff, conceived and designed the experiment, performed the experiment, analyzed the data, wrote the manuscript, prepared figures and tables, and reviewed drafts of the manuscript. Dr. Cynthia McKenzie conceived the experiment, contributed resources, provided field support through DFO staff, and reviewed drafts of the manuscript. Kiley Best conceived the experiment, assisted with field work, and reviewed drafts of the manuscript. Nicola Zargarpour assisted with field work, and reviewed drafts of the manuscript. Dr. Brett Favaro conceived and designed the experiment, contributed resources, supervised the experiment, provided advice and guidance throughout the experiment, and reviewed drafts of the manuscript.

Chapter 2: Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada

A version of this manuscript has been published in PeerJ, and is available at:

<https://peerj.com/articles/4223/>

Bergshoeff J.A., McKenzie, C.H., Best, K., Zargarpour, N., Favaro, B. 2018. Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada. PeerJ, 6:e4223. <https://doi.org/10.7717/peerj.4223>

2.1 Abstract:

The European green crab (*Carcinus maenas*) is a destructive marine invader that was first discovered in Newfoundland waters in 2007 and has since become established in nearshore ecosystems on the south and west coast of the island. Targeted fishing programs aimed at removing green crabs from invaded Newfoundland ecosystems use Fukui traps, but the capture efficiency of these traps has not been previously assessed. We assessed Fukui traps using *in situ* observation with underwater video cameras as they fished for green crabs. From these videos, we recorded the number of green crabs that approached the trap, the outcome of each entry attempt (successful entry or failed entry), and the number of exits from the trap. Across eight videos (73.0 h), we observed 1,226 green crab entry attempts, with only a 16% rate of successful entry from these attempts. Based on these observations we believe there is scope to improve the performance of the Fukui trap through modifications in order to achieve a higher catch-per-unit-effort (CPUE), maximizing trap usage for mitigation. Ultimately, a more efficient Fukui trap will help to control green crab populations in order to preserve the function and integrity of ecosystems invaded by this species.

2.2 Introduction

The European green crab, *Carcinus maenas* (Linnaeus, 1758) is a crustacean species native to European and North African coastlines (Williams, 1984). It has been ranked among 100 of the world's 'worst invasive alien species' by the International Union for Conservation of Nature (Lowe et al., 2000). In North America, current distributions of the European green crab (hereafter, green crab) on the west coast range from California, USA (Cohen, Carlton & Fountain, 1995; Behrens Yamada & Gillespie, 2008) up to British Columbia, Canada (Gillespie et al., 2007). On the east coast green crabs can be found from Virginia, USA (Williams, 1984) to Newfoundland, Canada (Blakeslee et al., 2010; McKenzie et al., 2011). Evidence suggests that green crab populations on the east coast are made up of both northern and southern genotypes that originated from two separate introduction events. First, the historical invasion of the northeastern United States in the early 1800's by green crabs originating from the southern United Kingdom (Say, 1817; Roman, 2006; Blakeslee et al., 2010). Second, an introduction into the Maritimes in the late 1980's by a more cold-tolerant population from the northern limit of the green crab's range in Europe (Roman, 2006; Blakeslee et al., 2010; DFO, 2011a).

The green crab was first discovered in the nearshore waters of Newfoundland in 2007, and has since become established across the southern and western coasts of the island (DFO, 2011a). Genetic analysis of Newfoundland green crab populations indicate a mixed ancestry of both the southern and northern genotypes, with a close relationship to the more cold-tolerant, northern population (Blakeslee et al., 2010; DFO, 2011a). Recent

findings show that green crab populations on the west coast of Newfoundland (i.e., St. George's Bay) are genetically different from those on the southeast coast (i.e., Placentia Bay), which could manifest themselves in different behaviours and invasion characteristics (Rossong et al., 2012; Jeffery et al., 2017). Furthermore, this genetic variability could also contribute to differences in catchability across Newfoundland.

The invasion is concerning because green crabs can destroy eelgrass beds (DFO, 2011a; Matheson et al., 2016), are voracious predators of bivalves (Ropes, 1968; Cohen, Carlton & Fountain, 1995; Klassen & Locke, 2007; Matheson & McKenzie, 2014), and compete with native species and other crustaceans for food and habitat (Cohen, Carlton & Fountain, 1995; Matheson & Gagnon, 2012). The impact of green crabs on eelgrass beds is particularly threatening as invasive species are one of the multiple stressors contributing to a global trend in seagrass decline (Orth et al., 2006). Eelgrass serves as important habitat for commercial species such as cod, herring, and lobster. Therefore, green crab invasions pose both an ecological and economic threat (Joseph, Schmidt & Gregory, 2013; Matheson et al., 2016).

The complete eradication of an invasive species in an aquatic environment is virtually impossible once the organism has become established, and may only be possible if the invasion is in a confined area and addressed shortly after arrival (Bax et al., 2002, 2003; Lodge et al., 2006). In Newfoundland, the complete eradication of green crabs is no longer considered an option. Therefore, efforts are now focused on mitigation to suppress invasive populations to slow their spread and minimize their negative effects (DFO, 2011b). These mitigation studies have found that the direct removal of green crabs

through focused trapping is one effective control technique, and has become the current method of conducting targeted removals of green crabs on both the east and west coast of Canada (DFO, 2011a,b; Duncombe & Therriault, 2017). Green crab removal efforts in Canada usually use Fukui traps (60 x 45 x 20 cm, 12 mm bar length square mesh, 45 cm expandable entry slit) which are practical for mitigation efforts as they are light-weight, collapsible, durable, and can be easily deployed from small boats or from shore.

Despite the widespread use of the Fukui trap for research, monitoring, and mitigation, there have been no formal investigations of the interactions between green crabs and the standard Fukui trap, and substantial knowledge gaps exist surrounding the trap's overall efficiency. In addition, it has been shown that green crab aggression and feeding behaviour can vary across sites, which may influence catch rates and the performance of the trap between areas (Rossong et al., 2012). The main objectives of this study were to evaluate the performance and efficiency of the Fukui trap in terms of its ability to catch green crabs, and to gain a better understanding of this capture process and how it may differ across sites in Newfoundland.

In this study, we used underwater video cameras to record footage of the traps as they actively fished for green crabs *in situ* across Newfoundland. Underwater video is the best way to understand the interactions between an animal and a piece of fishing gear, and is beneficial in determining the optimal design and use of this fishing gear (Favaro et al., 2012; Underwood, Winger & Legge, 2012). There is a growing body of literature on the use of cameras to better understand various types of fishing gears, including traps (alternatively referred to as pots) (Jury et al., 2001; Barber & Cobb, 2009; Bacheler et al.,

2013b; Favaro, Duff & Côté, 2013; Meintzer, Walsh & Favaro, 2017), trawls (Nguyen et al., 2014; Underwood et al., 2015), and hooks (He, 2003; Robbins et al., 2013). In the case of the Fukui trap, underwater video is an effective method to accurately assess the number of green crabs that approach the trap, the outcome of each attempt to enter the trap, and the likelihood that a green crab will remain inside the trap until it is retrieved.

Six steps have to be completed successfully for green crabs to be caught in a trap (Figure 2.1) (Favaro, Duff & Côté, 2014). First, they must be present in the area where the Fukui trap has been deployed. Second, they must be able to detect the presence of the trap, either visually or by detecting olfactory cues of the bait plume. Third, green crabs must approach the Fukui trap. Fourth, they must locate one of the entrances and make an entry attempt. Fifth, they must successfully complete that entry attempt in order to become captured. Sixth, they must remain in the trap until the gear is hauled (i.e., they must not exit). The use of underwater video cameras in this study enabled us to accurately evaluate steps three through six of the capture process (number of approaches to the trap, proportion of successful entry attempts, number of exits) in order to determine the effectiveness of the Fukui trap at catching green crabs. Furthermore, the use of underwater video allowed us to identify barriers that were inhibiting the capture process. This information will enable us to identify inefficiencies in the capture process that could be addressed through modifications to the fishing gear, so that future removal programs can be conducted more efficiently.

2.3 Methods

2.3.1 *Camera apparatus and equipment*

We used custom-built camera housings with Sony HDR-AS20 Action Cameras capable of recording 13-hour high-definition underwater videos (as described in Bergshoeff et al., 2017). We mounted each camera system to a wooden frame built around a standard Fukui trap. Using a large 114–165 mm diameter gear-clamp, the camera housing was centred above the trap, with the camera pointing downward to provide a top-down view of the trap and surrounding area (Figure 2.2). The camera was positioned at a height of 53 cm above the top of the trap and 74 cm above the ocean floor, creating a field of view (FOV) of approximately 81 cm by 150 cm when filming underwater. The wide-angle lens of the camera made it possible to view the entire trap, in addition to a buffer surrounding all edges of the trap (45 cm to the left and right edge of the trap, and 18 cm from the top and bottom edge). The wooden frame was weighted down with four 2.8 kg cement bricks in order to make it negatively buoyant and to prevent shifting due to currents and wave action. Finally, the rope attaching the trap to the surface float was marked in half-metre increments in order to determine the approximate depth of deployment.

An external lighting system was necessary for overnight trap deployments; therefore, each camera apparatus was equipped with two Light and Motion (Marina, California, USA) Gobe Plus flashlights with red LED light attachments (Gobe Focus Head). On low-power mode these flashlights had sufficient battery life to illuminate the entire night cycle. Many crustaceans are insensitive to wavelengths greater than 620 nm;

therefore, we used red lights with the goal of minimizing the behavioural impacts that may accompany full-spectrum light (Nguyen et al., 2017).

2.3.2 Field methods

We recorded underwater videos at six sites across Newfoundland during the summer of 2015 and one site during the summer of 2016 (Figure 2.3). We produced the map in Figure 2.3 using the ggmap package (Kahle & Wickham, 2013) in R (R Core Team, 2015). The sites were as follows:

1. Fair Haven (FH), Placentia Bay (June 9-11, 2015 & August 18-20, 2015)
2. Boat Harbour (BH), Placentia Bay (June 23-26, 2015)
3. Little Harbour East (LHE), Fortune Bay (June 22-23, 2015)
4. Little Port Harmon (PH), St. George's Bay (July 7-10, 2015)
5. Penguin Arm (PA), Bay of Islands (July 14-15, 2015)
6. Deer Arm (BB), Bonne Bay (July 11-14, 2015)
7. Fox Harbour (FX), Placentia Bay (June 30 – July 1, 2016).

Each of these shallow, coastal sites have known green crab populations, and consist of similar mixed mud, sand, and rock habitat. The video data from June 2016 in Fox Harbour, NL were collected as part of a complementary study that followed the same methods for recording videos, and we therefore included the results in our analysis.

At each site we followed a set procedure for deploying the camera traps. Prior to each deployment, the Fukui traps were baited with equal amounts of Atlantic herring (*Clupea harengus*), the standard bait used by Fisheries and Oceans Canada (hereafter, DFO) for green crab mitigation projects, in a perforated plastic bait container (Gillespie

et al., 2007; DFO, 2011b). The herring was thawed and cut into pieces, with approximately half of a fish placed into each bait container. Once the traps were baited, the camera equipment was secured inside the camera housing and mounted to the frame surrounding the Fukui trap. We used a wireless Sony RM-LVR1 Live View Remote to ensure that the camera and FOV were oriented correctly and to initiate recording prior to each trap deployment.

We typically deployed the traps close to shore (<50 m) using a small Zodiac boat. When we placed the traps in the water, we made sure that the camera housing entered the water horizontally in order to prevent air bubbles from becoming trapped on the housing's acrylic viewport. We deployed each trap no less than 1 m below the low tide water depth to prevent the camera apparatus from breaching the surface with the changing tides. Each camera trap was paired with a Fukui trap without an attached camera to examine whether the camera itself affected catch rates. The two traps within each pair were placed approximately 10 m apart based on other studies involving the Fukui traps (Gillespie et al., 2007; Behrens Yamada & Gillespie, 2008; Curtis et al., 2015). In total, two camera traps and two non-camera traps were set at each deployment. Sampling location, global positioning system (GPS) coordinates, time of day, depth, and weather information were recorded for each deployment. Traps were either deployed early in the day and retrieved in the evening (termed 'daytime deployments'), or deployed before sunset and retrieved the next morning (termed 'overnight deployments'). We aimed for each trap to be deployed for 12 h, but logistical factors such as weather and travel sometimes affected trap retrieval time adding variation to total soak time. These

logistical factors also meant that some traps were not deployed until the afternoon, and retrieved the following morning (termed ‘mixed deployments’).

When the traps were retrieved the catch was sorted, counted, and sexed. All bycatch species were visually identified to the lowest possible taxonomic level, recorded, and released as soon as possible. As per DFO recommendations, all captured green crabs were euthanized by freezing and disposed of in the Marine Institute’s waste disposal unit. Once the catch was processed, the camera equipment was reset, and the traps were prepared for re-deployment. We re-baited the traps with fresh herring before each new deployment.

The project was approved as a ‘Category A’ study by the Institutional Animal Care Committee at Memorial University as it involved only invertebrates (project # 15-02-BF), and all field research was conducted under experimental licenses NL-3133-15 and NL-3271-16 issued by DFO.

Throughout our manuscript, data description was done using the mean and standard deviation (SD). When reporting a mean, we included the SD in parentheses. When reporting a range, we included the mean and SD in parentheses.

2.3.3 Determining the effect of camera presence on catch

We built two linear mixed-effects models using the nlme package (Pinhero et al., 2017) in R (R Core Team, 2015) in order to test whether the presence of the camera had an effect on green crab catch. We analyzed a subset of the green crab catch data which included only Fair Haven, NL and Little Port Harmon, NL. All other sites were excluded from our subset due to either zero green crab catch, or low mean catch rates (Table 2.1).

We did not see any meaningful relationship between deployment duration and catch (Figure 2.4A, B). However, the soak times were not consistent between Fair Haven (range = 21.8 – 24.3 h; mean = 22.9 h; SD = 0.8) and Little Port Harmon (range = 7.4 – 14.1 h, mean = 11.1 h; SD = 2.8) (Figure 2.4C). To account for this, we created a separate model for each location because the underlying effect of soak time on catch was potentially unique to each site (Figure 2.4D). These two models tested the fixed effects of camera presence (i.e., camera present, camera absent) and duration on catch-per-deployment. We did not include deployment type (i.e., daytime, overnight, mixed) in our final models as the term was not significant in the Little Port Harmon model, and lacked sufficient factor levels in the Fair Haven model (mixed deployments only). Due to the paired nature of our design we designated each camera and non-camera pair as a single deployment, which was included in each model as a random effect. The residuals for both the Fair Haven and Little Port Harmon models met the assumptions for homogeneity, normality, and independence.

2.3.4 Video analysis

2.3.4.1 Video Selection

In order to determine which videos to analyze in-full, we first reviewed them according to a selection key (Supplementary Figure 2.1). This process involved evaluating the level of green crab activity in each video, as well as an assessment of the overall image quality. The activity level of each video was determined by counting the approximate number of green crabs present in the FOV at 35-min intervals and

calculating the overall mean across those intervals. The average number of green crabs in the FOV corresponded to the following activity levels: 0 = ‘none’; 0.1 – 5.0 = ‘low’; 5.1 – 10.0 = ‘medium’; 10.0 and above = ‘high’. If the activity level was determined to be ‘none’ or ‘low’ the video was disqualified. Our assessment of video quality was based on visibility of the trap due to particulate matter and lighting conditions. If the bottom panel (i.e., the floor) of the Fukui trap was clearly visible, as well as the entire periphery of the FOV, then the video quality was classified as ‘good’. If the bottom panel of the Fukui trap was clearly visible, but the periphery of the FOV was poorly lit, then the video quality was classified as ‘fair’. Finally, if the bottom panel of the Fukui trap was not visible due to lighting or particulate matter, the video quality was classified as ‘poor’. If the video quality was determined to be ‘poor’, the video was disqualified. Overall, in order to qualify for analysis each video required ‘medium’ or ‘high’ activity levels, as well as ‘fair’ or ‘good’ video quality.

2.3.4.2 Video analysis procedure

We used a standardized procedure to evaluate the video obtained during the 2015 and 2016 field seasons. Video files were viewed using VLC Media Player 2.2.4 on a 27-inch (68.6 cm) 16:9 (widescreen) flat screen monitor. For night videos, we used the sepia colour setting in VLC to reduce glare and eye-strain caused by the red lighting. Data were recorded in a spreadsheet. The analysis procedure involved characterizing the video by ‘events’ (both qualitative and quantitative) and recording the time during the video at which each event occurred.

We began analyzing the video as soon as the trap settled on the ocean floor after deployment. The FOV was divided into four sections in a clockwise manner (top = 1, right = 2, bottom = 3, left = 4). Every time an animal entered the FOV, we recorded the direction of approach (e.g., APP1, APP2), the species (e.g., GC for green crab, RC for rock crab), and the time as indicated by the VLC time counter. A rough estimate of size was made for each species (small, medium, or large); however, limited emphasis was placed on this information due to the potential for biases and size distortion depending on the distance of a green crab from the camera. We could not individually identify crabs as they entered and re-entered the FOV; therefore, the number of approaches by green crabs to the Fukui trap does not represent the absolute number of individual crabs that approached the trap.

We recorded each attempt to enter the trap, along with the time taken to complete or fail the attempt. For green crabs, an attempt was defined as when the entire body of the crab was inside the entry tunnel of either entrance 1 or entrance 2 (Figure 2.5). The time for each attempt was recorded until the entry was either successful (i.e., a green crab fully entered the trap) or failed (i.e., a green crab fully left the entrance tunnel). If an entry attempt failed, the predominant reason for failure was noted according to four common, reoccurring situations: 1) Agonism (AGON): some form of intraspecific or interspecific agonistic behaviour deterred or prevented the green crab from entering the trap, 2) Partial entry (PE): the green crab entered the entrance tunnel, but turned around and exited before contacting the trap entry slit, 3) Full entry (FE): the green crab fully entered the entrance tunnel and contacted the trap entry slit, but subsequently turned around and

exited, or 4) Difficulty completing entry (DCE): the green crab fully entered the entrance tunnel, but was unable to get through the trap entry slit in order to successfully complete the entry, and subsequently turned around and exited. Additionally, if a green crab was able to escape the trap after it had successfully entered, this was recorded as an exit.

If a notable behaviour occurred that was not part of our core observation framework (e.g., predation) we recorded the time and context of the event. We focused on behavioural interactions outside of the trap instead of green crabs already inside the trap, which could be seen as an artificial environment influencing behaviour.

2.3.5 Regional performance of the Fukui trap

Recently, it has been shown that genetically different green crab populations exist within Newfoundland which could influence behaviour and catchability (Rosson et al., 2012; Jeffery et al., 2017). We compared video analysis results between St. George's Bay (i.e., Little Port Harmon) on the west coast of Newfoundland, and Placentia Bay (i.e., Fair Haven and Fox Harbour) on the southeast coast in order to examine regional differences in the performance of the Fukui trap. When comparing these regional differences, we focused on parameters related directly to the interactions of green crabs with the Fukui trap. This allowed us to evaluate whether variations in regional green crab behaviour had an impact on Fukui trap performance. The two parameters we examined were the elapsed time for successful and failed entry attempts, and the frequency of these attempts.

We used a generalized linear mixed model (GLMM) to test whether there was an interaction between the elapsed time for successful or failed green crab entry attempts,

and region. To build our model we used the lme4 package (Bates et al., 2017) in R (R Core Team, 2015). The distribution of elapsed entry attempt time was best explained by a negative binomial distribution. The fixed covariates in our model were *outcome* (categorical with two levels: success, failure) and *region* (categorical with two levels: west, southeast). We included *video ID* as a random effect to account for dependency among observations from the same video. We verified the assumptions of our model by plotting residuals versus fitted values, and testing for overdispersion.

We assessed whether there was an association between the frequency of entry attempt outcomes (i.e., successful entry, failed entry) and region (i.e., west, southeast) using a chi-squared test. We set the level of statistical significance for rejecting the null hypothesis at $\alpha < 0.05$.

2.4 Results

2.4.1 Field deployments

During the 2015 field season, a total of 39 camera traps and 39 traps without cameras were deployed (total $n = 78$) across the six field sites. Trap deployment times ranged from 2.7 to 24.4 h (mean = 14.2 h; SD = 6.1). We collected 37 videos in total. Two of the 39 videos failed due to partial flooding of the camera housing. Recording duration of videos ranged from 2.7 to 13.0 h (mean = 11.2 h; SD = 2.7). The inconsistency in deployment durations can be attributed to a combination of logistical challenges getting to-and-from the site and inclement weather preventing retrieval of the gear.

Both the fishing effort and the number of green crabs caught per trap varied across the six study sites visited in 2015, with all but two of the sites (Fair Haven and Little Port Harmon) exhibiting a mean catch of less than 10 green crabs per deployment (Table 2.1). Generally, bycatch using the Fukui trap was minimal. The most common occurrence of bycatch was rock crab (*Cancer irroratus*) in Boat Harbour and Bonne Bay (Table 2.2).

2.4.2 Camera effects

We found the presence of the camera had no significant impact on catch at both Fair Haven ($\beta_1 = 19.409$, S.E. = 46.797, $t = 0.415$, $p = 0.693$) and Little Port Harmon ($\beta_1 = -15.951$, S.E. = 16.970, $t = -1.268$, $p = 0.273$) based on our subset of catch data from these two locations. The effect size, β_1 , can be interpreted as an increase of 19 crabs per trap when a camera is present at Fair Haven, and a decrease in 16 crabs per trap when the camera is present at Little Port Harmon, both relative to non-camera traps. Camera traps fished in Fair Haven ($n = 8$) caught between 10 and 299 green crabs (mean = 140.9 crabs; SD = 99.6), and non-camera traps fished in Fair Haven ($n = 8$) caught between 18 and 232 green crabs (mean = 122.6 crabs; SD = 80.9). Camera traps fished in Little Port Harmon ($n = 6$) caught between 3 and 74 green crabs (mean = 26.3 crabs; SD = 26.3), and non-camera traps ($n = 6$) fished in Little Port Harmon caught between 0 and 102 green crabs (mean = 42.5 crabs; SD = 34.4).

2.4.3 Video analysis

Using the video selection key (Supplementary Figure 2.1), we determined that 8 of the 37 collected videos were suitable for complete analysis. The majority of videos

that were rejected from the analysis process showed no or ‘low’ green crab activity. Overall, videos were clear and well illuminated. However, videos collected at night under red illumination were dim around the periphery of the FOV (Figure 2.2). Additionally, videos collected in Fair Haven in late-August, 2015 were disqualified due to ‘poor’ quality caused by excessive turbidity and suspended particulate material in the shallow bay in which we were trapping.

Results from the eight videos that were analyzed can be examined in Table 2.3. The variability among videos, and the range of green crab activity levels across each site are illustrated in Figure 2.6. In total, we observed 2,373 green crab approaches to the trap over the course of eight videos (73.0 h), and 351 by other species (Figure 2.6A). During these videos, green crabs comprised 86.0% (SD = 10.3) of all approaches to the trap, and it took 3.5 min (SD = 3.4) on average for the first green crab to approach the trap (range: 0.9 – 11.1 min). We observed an average of 35.7 green crab approaches per hour (SD = 18.2) across all eight videos. Only 8.1% (SD = 5.2) of the 2,373 green crab approaches resulted in a successful entry into the Fukui trap. No green crab exits were observed.

We observed a total of 1,226 green crabs make attempts to enter the Fukui trap across all sites (Figure 2.6B), as well as 30 attempts by other species. On average, there were 18.0 entry attempts per hour (SD = 8.9), and 52.5% (SD = 10.9) of the green crabs that approached the trap made entry attempts. In total, 181 green crabs made successful entry attempts (Figure 2.6C). The success rate for each video ranged from 0.9 – 32.5%, with a mean of 16.0% (SD = 11.4). On average, it took a green crab 140.3 s (SD = 147.8) to successfully enter the Fukui trap during an entry attempt (range: 8 – 837 s), while it

took an average of 126.1 s (SD = 200.2) before a green crab would fail an entry attempt (range: 3 – 2789 s).

We observed 1,045 failed entry attempts in total. For each of the eight videos, the average proportion of failed entry attempts was 84.0% (SD = 11.4). This proportion can be further broken down according to the four most common reasons for failure (Figure 2.7).

First, 4.0% (SD = 2.4) of all entry attempts failed due to some sort of agonistic behaviour (AGON; $n = 51$) preventing the green crab from entering the trap. If two green crabs were making a simultaneous entry attempt, agonistic behaviour between them would often cause either crab to abandon the entry attempt. We also observed crabs already inside of the entry tunnel deterring other crabs from entering. This agonistic behaviour was not limited to crabs outside of the trap; green crabs that were already successfully captured would occasionally attempt to deter other crabs from entering the trap.

Second, 20.0% (SD = 12.2) of all entry attempts failed because the green crab entered the entry tunnel, but only made a partial entry (PE; $n = 209$) before exiting. There was often no obvious behaviour driving partial entry attempts.

Third, 15.5% (SD = 7.4) of all entry attempts failed after the green crab fully entered the entrance tunnel and contacted the entry slit, but subsequently turned around (FE; $n = 215$). As green crabs moved further inside the wedge-shaped entry tunnel towards the entry slit, their movement would become more restricted. Occasionally, the pereopod of a green crab would hook the mesh (1cm x 1cm) on the top or side panel of

the entrance tunnel, causing the crab to become redirected outside of the trap, instead of further inside.

Finally, 44.5% (SD = 14.4) of all entry attempts failed because the green crab had difficulty getting through the trap entry slit in order to complete the entry (DCE; $n = 570$). The amount of time spent by a green crab attempting to pass through the trap entry slit ranged from 19 to 2,789 s (mean = 194.5 s; SD = 249.3). The sharp pereopods of green crabs would often become entangled or caught in the mesh of the Fukui trap, inhibiting successful entry. Similarly, the five anterolateral spines on either side of the green crabs' eyes would often catch on the mesh of the entry slit during entry attempts. Furthermore, even without getting caught in the mesh of the trap, the entry slit was often too tight for the crabs to easily slip through, causing them to become stuck or entangled, and ultimately fail the entry attempt. If a crab was able to reach one of its pereopods or chelipeds through the trap entry slit, there was often nothing to grab hold of in order to pull itself through the tight-fitting entry slit, resulting in a failed entry attempt.

Based on the 181 successful entry attempts, we observed several scenarios that assisted green crabs in making a successful entry. If a crab approached the entrance tunnel at a fast pace, it was often able to use this momentum to push through the restrictive trap entry slit with minimal effort. Similarly, if a green crab approached the entry slit backwards, this would prevent the forward-facing anterolateral spines of the carapace from becoming caught in the mesh. This would allow green crabs to enter the trap more easily. In other situations, crabs would struggle for sustained periods of time to pass through the trap entry slit, with some eventually achieving success. We also

observed crabs using the bait container hanging in the centre of the trap to assist in pulling themselves through the entry slit.

2.4.4 Regional performance of the Fukui trap

The performance of the Fukui trap remained consistent across Newfoundland, regardless of region (i.e., Fox Harbour and Fair Haven in southeastern Newfoundland, Little Port Harmon in western Newfoundland). We found there was no significant difference in elapsed entry attempt time between regions ($\beta_1 = 0.231$, S.E. = 0.260, $t = 0.889$, $p = 0.374$), and we found no significant interaction between entry attempt outcome and region ($\beta_1 = 0.046$, S.E. = 0.159, $t = 0.287$, $p = 0.774$). From our video data, the average elapsed time for successful entry attempts in the west was 163.7 s (SD = 169.5), and 120.5 s (SD = 124.1) in the southeast. The average elapsed time for failed entry attempts in the west was 129.8 s (SD = 195.4), and 122.5 s (SD = 204.8) in the southeast. Through our chi-squared test, we failed to reject the null hypothesis that there was no association between the frequency of entry attempt outcomes and region ($\chi^2 = 0.558$, $df = 1$, $p = 0.455$). Based on all entry attempts within each region, the proportion of successful entry attempts was 14% in the west, and 16% in the southeast.

2.5 Discussion

2.5.1 Video quality

In this study, we found underwater video to be an effective means of evaluating the Fukui trap as it actively fishes for invasive green crabs *in situ*, providing information that could not be inferred from catch data alone. However, there are inherent challenges

associated with the collection of data from video recordings. First, the illumination during overnight deployments was dim around the periphery of the FOV and the use of red lights had an impact on image quality due to high absorption of this frequency in water (Williams et al., 2014). Therefore, the number of approaches recorded during these deployments may have been less accurate than daytime deployments. This is a common issue when recording video in low-light environments (Underwood, Winger & Legge, 2012; Favaro, Duff & Côté, 2014). Both entry tunnels and the entry slits were clearly illuminated during overnight deployments. Therefore, the accuracy of entry attempt data remained consistent across all deployments. Second, we were limited to videos collected in June and July due to poor visibility caused by increased water temperature in mid-August. The videos collected in Fair Haven in August 2015 had to be disqualified due to excessive turbidity and suspended particulate material. Finally, as green crabs accumulated inside the Fukui trap, it became more difficult to track individual crabs as they made entry attempts. As the density inside the trap increased, our line-of-sight was often obstructed by green crabs already inside the trap. This may have had an effect on the number of entry attempts recorded in videos with high green crab densities, which could have ultimately influenced our calculations of entry attempt proportions.

2.5.2 Evaluation of the six-step capture process

Through our video analysis, we have gained considerable insight into the performance of the standard Fukui trap as a tool for green crab mitigation, as well as the behaviour of the green crab in relation to the trap itself, other species, and other green

crabs. These findings can be summarized using the framework of the six-step capture process (Figure 2.1).

Step 1 – Green crabs must be present in the ecosystem

The number of green crabs present in the areas where we deployed Fukui traps varied. Effective trapping requires that green crabs be present in sufficient numbers within the area being fished. Despite anecdotal evidence of established green crab populations at all sites sampled in 2015, most of our green crab catch was limited to either Fair Haven or Little Port Harmon (Table 2.1). We hypothesize that the low catch rates at the other locations could be attributed to environmental factors. Newfoundland experienced a prolonged winter in 2014 – 2015 with above normal ice extent, followed by a late spring warming (DFO, 2016). It has been shown that unusually low winter temperatures can result in mass mortality of adult green crabs, and poor recruitment (Crisp, 1964; Welch, 1968; Berrill, 1982; Beukema, 1991). These low temperatures could have had an impact on green crab populations, producing less catch in certain areas than was seen in previous years (Welch, 1968; Behrens Yamada & Kosro, 2010).

When deploying the camera apparatus, we had to ensure that the camera would not breach the water's surface with the changing tides. To account for this, we deployed the cameras approximately 1 m below low tide depth. Green crabs are most commonly found in depths ranging from high tide levels to 5 – 6 m, and have been reported at depths of up to 60 m (Crothers J. H., 1968; Klassen & Locke, 2007). Despite the minimum depth limitation dictated by the height of the camera above the Fukui trap, we are confident that the placement of our traps was sufficient to catch green crabs if they

were present at each trapping location. Furthermore, we had no reason to believe that the minor variations in the depth of our camera traps would have had any significant impact on the behaviour of green crabs in relation to the Fukui trap.

Bycatch at each location was generally low, particularly in areas where large numbers of green crabs were present (Table 2.2). This suggests that the Fukui trap has a minimal impact on native species, and is an appropriate trap for targeting green crabs in areas where other species are present. Presumed predation by green crabs causing bycatch mortality was rare, and limited to soft-bodied species such as winter flounder (*Pseudopleuronectes americanus*), cunner (*Tautoglabrus adspersus*), and sculpin (*Myoxocephalus sp.*) in Fukui traps containing large quantities of green crabs. We saw no mortality of rock crabs (*Cancer irroratus*) or American eel (*Anguilla rostrata*), and all living bycatch present in the Fukui trap upon retrieval was released alive.

Step 2 – Green crabs must detect the trap

Green crabs primarily use chemoreception to locate a food source (Shelton & Mackie, 1971). It did not take long for green crabs to locate and approach our baited Fukui traps after they settled on the seafloor. On average, the first green crab would approach the Fukui trap within four min. Therefore, if green crabs were present in the area where the trap was deployed, then the olfactory cues from the herring functioned as effective bait.

In our study, we did not examine the effects of water direction. However, other experiments on crustaceans have demonstrated that aligning a trap's entrances with the current can improve catch by leading the target species into the trap as they follow the

bait plume (Miller, 1978; Vazquez Archdale et al., 2003). For this reason, when targeting green crabs with the Fukui trap it may benefit catchability to align the entrance tunnels with the water direction, so that crabs can follow the bait's odour trail directly into the trap.

Step 3 – Green crabs must approach the trap

We observed a range of different behaviours associated with green crabs approaching the Fukui trap. Some green crabs would make an entry attempt right away, entering the camera's FOV and proceeding directly to the entrance tunnel. In other instances, green crabs would move around the trap for long periods of time before discovering the entrance tunnel, or beginning an entry attempt. We frequently observed agonistic behaviour on and around the Fukui trap, especially once green crabs began to accumulate in the area. Green crabs would often cluster on top of the trap, situating themselves above the bait container (hanging inside the centre of the trap) as if they were guarding a food source, a behaviour that has been noted with Dungeness crab (*Metacarcinus magister*) (Barber & Cobb, 2009). This behaviour would result in confrontations between green crabs as they fought to either defend their position, or to displace the green crab guarding the bait. It was common to witness one green crab pursuing another around the trap, or to observe one crab grasping and immobilizing another. Size did not appear related to which green crab was the aggressor. Green crabs not only exhibited intraspecific agonistic behaviours, but often engaged with other species near the trap. It was not uncommon for green crabs to display aggressive behaviour towards a larger fish species, such as winter flounder.

Because we could not individually identify crabs as they entered and re-entered the FOV, the number of approaches by green crabs to the Fukui trap does not represent the absolute number of individual crabs that approached the trap. This is a common challenge associated *in situ* camera studies (Favaro, Duff & Côté, 2014). Despite this caveat, every entry attempt we observed can be considered a unique event, regardless of whether a green crab approached multiple times. If a target species repeatedly approaches a piece of fishing gear, yet fails to be captured, this suggests a fundamental problem with the fishing gear itself that must be addressed. Furthermore, Miller (1978) demonstrated that unless a trap is efficient at capturing crabs shortly after they approach a trap, they will begin to accumulate around the trap. This will increase the frequency of agonistic interactions, causing many crabs to flee from the trap, reducing the capture efficiency. Therefore, for a trap to maximize efficiency, it must successfully capture a target species shortly after it approaches.

Step 4 – Green crabs must make an entry attempt

A total of 1,226 green crabs made entry attempts, of which the majority were unsuccessful ($n = 1,045$). We repeatedly observed four scenarios that resulted in failed entry attempts (i.e., AGON, PE, FE, DCE). These reoccurring failure scenarios occurred across all eight videos, demonstrating that both green crab behaviour, and Fukui trap performance issues remained consistent, regardless of location.

The least common reason for failed entry attempts was intraspecific and interspecific agonistic behaviour, which deterred or prevented green crabs from entering the Fukui trap. Aggressive behaviour is common in invasive species, allowing them to

dominate over native species (Rehage & Sih, 2004; Pintor et al., 2008; Weis, 2010). The green crab is no exception, and is known for exhibiting both intraspecific and interspecific agonistic behaviour (Rosson et al., 2006; Klassen & Locke, 2007; Souza et al., 2011). This agonistic behaviour between green crabs has been shown to deter entry into baited traps (Crothers J. H., 1968; Gillespie et al., 2015). Similar behaviour has been documented in red rock crab (*Cancer productus*), Dungeness crab (*Metacarcinus magister*), and American lobster (*Homarus americanus*) where they have been observed guarding the entrances to traps, or using their bodies to prevent other individuals from entering the trap (Miller, 1978; Jury et al., 2001; Barber & Cobb, 2009). We also observed this behaviour; however, these events only comprised 4% of all failed attempts, suggesting that it has a minimal impact on overall catchability.

Partial and full entry attempts occurred when green crabs gained access to the entrance tunnels, but did not make an active effort to pass through the trap entry slits. There was little empirical evidence to explain these attempts beyond physical interactions between green crabs and the Fukui trap. The pereopods of green crabs could easily pass through the mesh of the Fukui trap, which would often cause them to become entangled or reoriented during entry attempts. Furthermore, the entry tunnels of a Fukui trap narrow towards the entrance slit. This limited the mobility of green crabs, and increased the likelihood that their pereopods would become entangled as they advanced further inside the entrance tunnel. This influenced the direction and orientation of the crab, and made it less likely that they would discover the entry slit in order to gain access to the inside of the trap.

The most common failure scenario occurred when a green crab had difficulty completing the entry attempt. This was characterized by the green crabs experiencing varying degrees of difficulty passing through the entry slit of the trap, and subsequently abandoning the attempt. The Fukui trap is designed so that a crab must force themselves through the entry slit, which remains tightly closed in its default position. However, even the most determined green crabs were often unable to enter the Fukui trap through these entry slits. A combination of mesh size and the restrictive opening of the trap entry slit made successful entries difficult. These same issues have been documented in a similar study with traps meant to target the Japanese rock crab (*Charybdis japonica*) (Vazquez Archdale et al., 2003). In this study, Archdale *et al.* observed crabs becoming entangled in the trap's netting material by their chelipeds and the spines on their carapace. They observed that forward-facing entry attempts would frequently result in entanglement, and difficulty in entering the trap. Furthermore, they observed that the trap's tight, narrow entry slits prevented crabs from squeezing in, forcing them to abandon entry attempts. For green crabs attempting to enter the Fukui trap, the predominance of DCE events suggests that the low catch rates are largely influenced by issues with the trap design itself, and not the behaviour of green crabs.

Step 5 – Green crabs must successfully enter the trap

Across all videos, we witnessed a total of 181 green crabs successfully enter the Fukui trap, suggesting that the capture efficiency of the trap is low. Successful green crabs were perseverant, often struggling for long periods of time before maneuvering themselves through the restrictive trap entry slit. Certain entry strategies appeared to

assist green crabs in successfully entering the Fukui trap, and body orientation was an important factor in facilitating successful entries. Most successful entries occurred when green crabs approached the entry slit sideways or backwards. In doing so, they were less prone to becoming entangled in the mesh as they pushed their way into the trap. These same entry strategies have been documented in Japanese rock crabs attempting to enter baited traps (Archdale, Kariyazono & Añasco, 2006).

The force required to gain access to the Fukui trap would also make it challenging for green crabs to successfully enter the trap. Surprisingly, the bait container located in the centre of the trap would occasionally assist green crabs in making successful entry attempts. The tension of the trap entry slit made it difficult for green crabs to push themselves through; however, if they were able to make it partially inside the trap, grasping the bait container would often allow them to pull themselves the rest of the way. This suggests that Fukui trap design would benefit from a proprietary mechanism to assist green crabs in pulling themselves into the trap.

There was great variability in success rates between videos, ranging from only 1% up to 33% (Table 2.3). When compared to similar studies of baited traps, the proportion of successful entry attempts into the Fukui trap is low. For example, traps used to capture Atlantic cod (*Gadus morhua*) and spot prawns (*Pandalus platyceros*) have successful entry attempt proportions of 22% and 46%, respectively (Favaro, Duff & Côté, 2014; Meintzer, Walsh & Favaro, 2017).

Furthermore, there was a disconnect between attraction to the trap and final catch. The number of approaches was positively correlated with entry attempts, demonstrating

that if there were many approaches to the trap, there were generally many entry attempts (Figure 2.6A and 2.6B). The large number of attempts seen in Figure 2.6B indicates that green crabs were actively trying to enter the Fukui trap. However, Figure 2.6C shows that this does not necessarily reflect how many green crabs were actually captured.

Figure 2.6C demonstrates that catch is not an accurate representation of entry attempt effort, as the success rate varied widely. Certain videos (e.g., PH5) had many green crab entry attempts, resulting in comparatively high catch. However, some videos (e.g., FH3, PH1) had many approaches and attempts, yet caught very few crabs. We hypothesize that the varying success rates may have been due to the condition of the specific Fukui trap used. For example, if the metal frame of the trap was distorted in such a way that the tension of the entry slit was altered, this could affect how well a green crab is able to enter the trap. Alternatively, if the mesh of the trap is worn or sagging, this could promote successful entries by making the entry slit less restrictive. Although we did not record the condition of the Fukui traps used in our study, future experiments should test the performance of specific traps as a factor that could influence catch. This hypothesis emphasizes the importance of regularly inspecting the condition of the Fukui trap in order to promote successful entry attempts.

The variable success rates not only suggest there may be a fundamental problem with the design of the Fukui trap, but that final catch does not necessarily reflect the abundance of green crabs in the vicinity of the trap at the time of deployment. Over the course of a deployment, many green crabs may attempt to enter a trap. However, as we have shown in this study, this effort is not necessarily reflected in the number of crabs

that are captured. This suggests that final catch could produce a biased perception of low green crab abundance in the area being fished. Other studies of crustacean catchability have demonstrated that traps can lead to biased estimates of CPUE and abundance (Murray & Seed, 2010; Kersey Sturdivant & Clark, 2011; Watson & Jury, 2013). For green crabs, local abundance is often estimated by catch rate (Gillespie et al., 2007; Duncombe & Therriault, 2017). From an invasive species management perspective, this shows that there may be more green crabs in an area than is suggested by catch data alone, emphasising the importance of not relying exclusively on catch data to estimate green crab populations in invaded areas.

Step 6 – Green crab must not exit the trap

Over the 73 h of video we analyzed, we did not observe a single escape from the Fukui trap, demonstrating that although it is difficult to enter the trap, once inside there is very little chance of a green crab escaping. However, it should be noted that we were not always able to retrieve the trap before the end of the video recording. Therefore, our final catch numbers do not necessarily correspond to what was observed in the video. Given the low rate of successful entry, the benefits of a highly secure trap that prevents escapes are lost when compared to the potential number of green crabs that could be captured if the entrance to the trap was less restrictive to begin with. To be more efficient, the Fukui trap needs to have a balance between effective catch and the risk of potential escapes.

2.5.3 Regional performance of the Fukui trap

The green crab is considered a global invader, and has established populations on almost every continent around the globe (Behrens Yamada, 2001; Carlton & Cohen,

2003). The expansive distribution of invasive green crab populations in North America alone, coupled with variations in genetic origin, suggests that there may not be a one-size-fits-all approach when responding to green crab invasions. That being said, the Fukui trap is being used on both the east (Matheson & Gagnon, 2012; Rossong et al., 2012; McNive, Quijon & Mitchell, 2013; Best, McKenzie & Couturier, 2014) and west (Behrens Yamada et al., 2005; Jensen, McDonald & Armstrong, 2007; Behrens Yamada & Gillespie, 2008; Duncombe & Therriault, 2017) coasts of North America, and remains the trap of choice for green crab mitigation due to its relative effectiveness, durability, and ease-of-use compared with other traps (Cynthia H. McKenzie, pers. comm., April 2, 2015).

In Newfoundland, we anticipated that genetic differences in aggression and foraging behaviour might influence how green crabs interacted with the Fukui trap. However, we saw little variation in the performance of the Fukui trap from one study site to the next, and there was no statistically significant differences in trap efficiency between regions. This suggests that the factors that contribute to high entry attempt failure, and therefore limit catch efficiency, are underlying problems with the Fukui trap itself and are not influenced by behavioural variations in local green crab populations. If these underlying factors that limit catch efficiency can be addressed and corrected, then we expect that catch efficiency can be improved wherever Fukui traps are being used as a mitigation tool, regardless of genetic differences and regional green crab characteristics.

2.5.4 Efficiency and modification

Only 16.0% of green crab entry attempts were successful, demonstrating that there is much room for improvement in the performance and efficiency of the Fukui trap. Still, the Fukui trap is a common choice for green crab mitigation across Canada, and intensive trapping has proven to be an effective technique for reducing green crab populations (Gillespie et al., 2007; DFO, 2011a,b). It has been shown that continuous trapping can cause a demographic shift towards a younger population, with reduced body mass and reproductive potential (Duncombe & Therriault, 2017). Furthermore, continuous trapping can gradually reduce the average carapace width of green crabs in an invaded area by removing larger individuals from the population (Duncombe & Therriault, 2017). This size decrease causes a shift in the ecological role of green crabs from primary predators, to potential prey for native shorebirds and crustaceans (DFO, 2011a). Furthermore, it has been shown that in areas where intensive trapping has occurred that the abundance of native species increases over time (e.g., rock crabs) (DFO, 2011a). Therefore, despite the limitations of the Fukui trap, it remains an important tool for reducing green crab populations in invaded ecosystems.

Based on our video observations, we believe there is scope to develop an improved Fukui trap that will facilitate the entry of green crabs into the trap. The problems associated with the design of the Fukui trap are predominately mechanical issues, and can likely be addressed through modifications. We propose three simple modifications that would likely improve the efficiency of the Fukui trap: First, the entry slit of the trap needs to be expanded slightly to allow green crabs to pass through more

freely. This could be accomplished using string, cable ties etc. to secure the entry slits in a partially-opened position. Second, the Fukui trap entrance tunnels could be constructed using a smaller mesh that would prevent green crabs from becoming entangled or snagged during entry attempts. This could quickly be accomplished by overlaying the existing mesh with a finer mesh, and securing it in place. Finally, green crabs would benefit from a fixed object on the inside of the Fukui trap that they could grasp in order to assist in pulling their bodies through the entry slit. This could be accomplished by simply affixing a piece of string, wire, mesh etc. across the width of the trap, on the interior side of the entrance slit. In addition to these design modifications, future studies could also test whether the addition of artificial lighting to the Fukui trap can be used to improve green crab CPUE, as seen with snow crab (*Chionoecetes opilio*) traps (Nguyen et al., 2017).

Any modifications to the Fukui trap would have to be tested to quantify the trade-offs of an altered trap design. If modifications were to alter the restrictive entry slit, this could increase the proportion of successful green crab entry attempts, but it could also impact retention (i.e., cause an increase in green crab exits). Furthermore, it is possible that a Fukui trap modified to capture more green crabs, may also catch more bycatch. However, if these design modifications are found to be effective, and the negative trade-offs are minimal, then this will greatly increase the number of green crabs that are removed from invaded ecosystems during mitigation efforts. Additionally, a more efficient Fukui trap will mean higher CPUE, maximizing trap usage for mitigation and control. Ultimately, a more efficient Fukui trap will help to control green crab

populations in order to preserve the function and integrity of ecosystems invaded by the green crab.

2.6 Conclusion

Our study represents the first formal investigation into the performance of the Fukui trap as a mitigation tool for the invasive green crab in Newfoundland. Our use of underwater video was a novel approach that allowed us to accurately determine the capture efficiency of these traps in a way that would be unachievable from catch data alone. Through the use of underwater video, we were able to gain insight into the efficiency of the Fukui trap, as well as the interactions that occur around and inside these traps as they are actively fished for green crab *in-situ*. Although our results revealed the rate of successful entries into the Fukui trap was low, we are confident that the mechanical inefficiencies of the trap can be addressed through simple modifications that will increase their CPUE. Furthermore, we were able to conclude that the underlying mechanisms contributing to low capture efficiency remained consistent regardless of the region or the local green crab population. The versatility of the Fukui trap as a control method for green crabs has contributed to its widespread use on both the east and west coast of Canada. Therefore, if the performance and efficiency of the Fukui trap can be improved then this will benefit green crab mitigation efforts wherever these traps are being used.

2.7 Tables

Table 2.1. Summary of green crabs caught at each study site in 2015.

Location	Deployments (n)	Mean catch	Std. Dev.	Min. catch	Max. catch	Total catch
Fair Haven	16	131.8	88.2	10	299	2108
Little Port Harmon	12	34.4	30.4	0	102	413
Little Harbour East	4	0.5	1	0	2	2
Penguin Arm	4	0	0	0	0	0
Bonne Bay	20	0.3	0.6	0	2	5
Boat Harbour	22	8.6	34.8	0	164	188
All Sites	78	34.8	67.5	0	299	2716

Table 2.2. Summary of all bycatch species caught at each study site in 2015.

The number of green crabs caught at each site has also been included for comparison purposes.

	Fair Haven	Little Port Harmon	Boat Harbour	Little Harbour East	Bonne Bay	Penguin Arm
Rock crab (<i>Cancer irroratus</i>)	0	2	116	0	84	4
Cunner (<i>Tautogolabrus adspersus</i>)	0	0	8	0	39	7
Winter flounder (<i>Pseudopleuronectes americanus</i>)	1	2	3	0	1	2
Sculpin sp. (<i>Myoxocephalus sp.</i>)	0	0	0	0	2	2
American eel (<i>Anguilla rostrata</i>)	0	1	0	0	0	1
Green crab (<i>Carcinus maenas</i>)	2108	413	188	2	5	0

Table 2.3. Summary of data from each video that was analyzed.

Video code represents the individual deployment of a camera-equipped Fukui trap at either Fair Haven (*FH*), Little Port Harmon (*PH*), or Fox Harbour (*FX*). Column headers are define as follows: video code (*Vid*), deployment date (mm-dd-yy) (*Date*), video duration (h) (*Dur*), green crab approaches (#) (*App GC*), green crab entry attempts (#) (*Att GC*), successful entries by green crabs (#) (*Succ GC*), exits by green crabs (#) (*Exit GC*), green crab success rate (%) (*Succ rate GC*), approaches by other species (#) (*App other*), entry attempts by other species (#) (*Att other*), successful entries by other species (#) (*Succ other*).

Vid	Date	Dur	App GC	Att GC	Succ GC	Exit GC	Succ rate GC	App other	Att other	Succ other
FH1	06/09/15	7.7	146	82	5	0	6.1	46	15	1
FH2	06/09/15	8.3	288	113	35	0	31.0	57	0	0
FH3	06/10/15	6.5	402	213	2	0	0.9	83	6	0
FH4	06/10/15	6.5	255	117	38	0	32.5	48	5	1
PH1	07/07/15	7.9	453	191	13	0	6.8	16	0	0
PH5	07/09/15	10.3	425	270	50	0	18.5	16	1	1
PH6	07/09/15	13.0	191	136	20	0	14.7	81	2	0
FX1	06/30/16	13.0	213	104	18	0	17.3	4	1	0

2.8 Figures

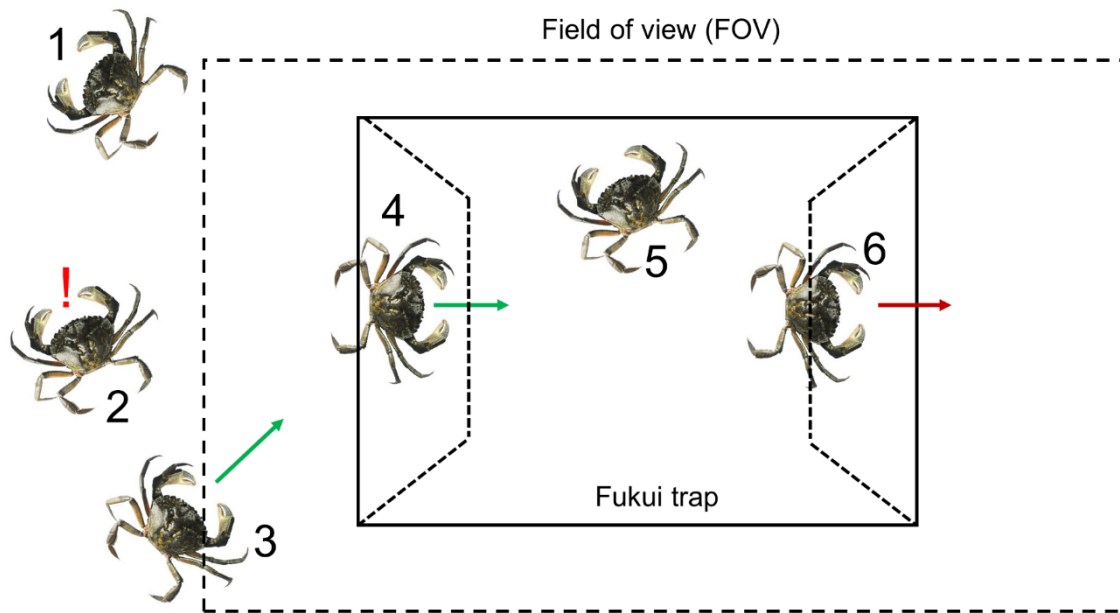


Figure 2.1. A visual representation of the six steps required for a green crab to be captured.

The numbers indicate the step in the capture process: 1) Presence, 2) Detection, 3) Approach, 4) Attempt, 5) Capture, 6) Exit.

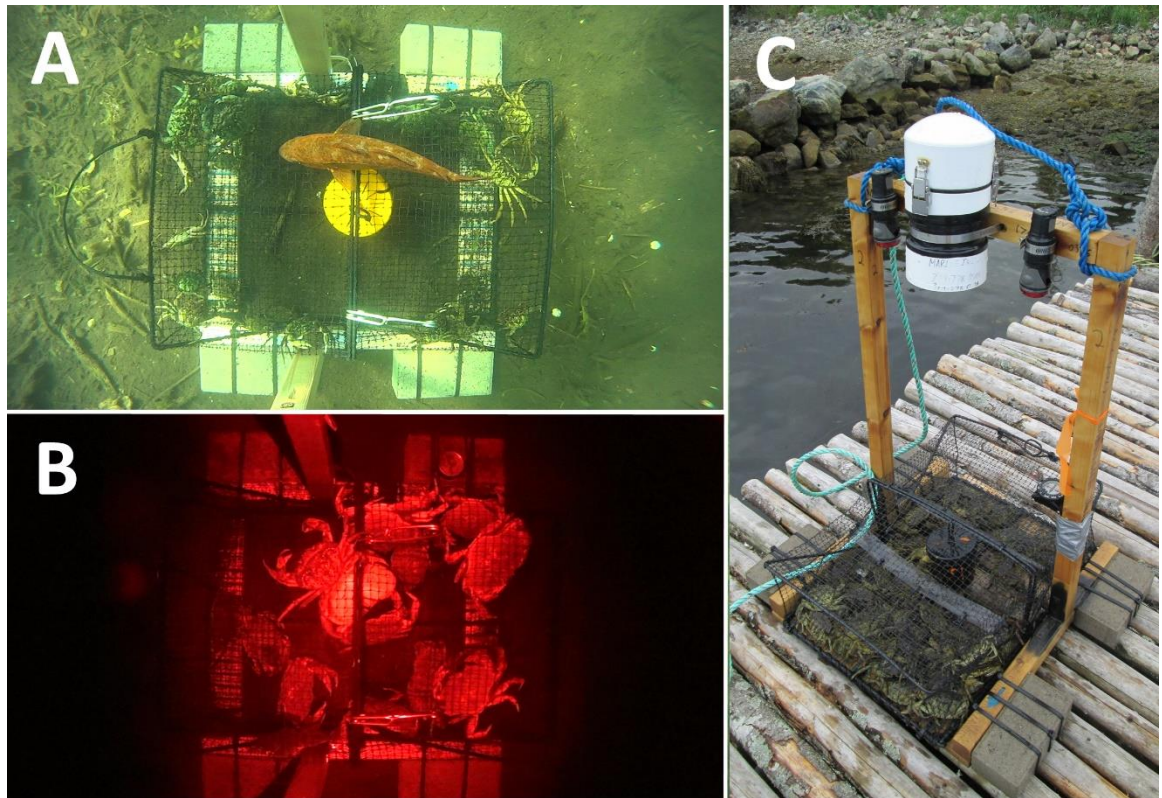


Figure 2.2. The camera frame constructed around a Fukui trap and its field of view. A top-down view of the Fukui trap recorded during a daytime deployment (A) and overnight deployment (B). The entire camera apparatus mounted to a Fukui trap (C).

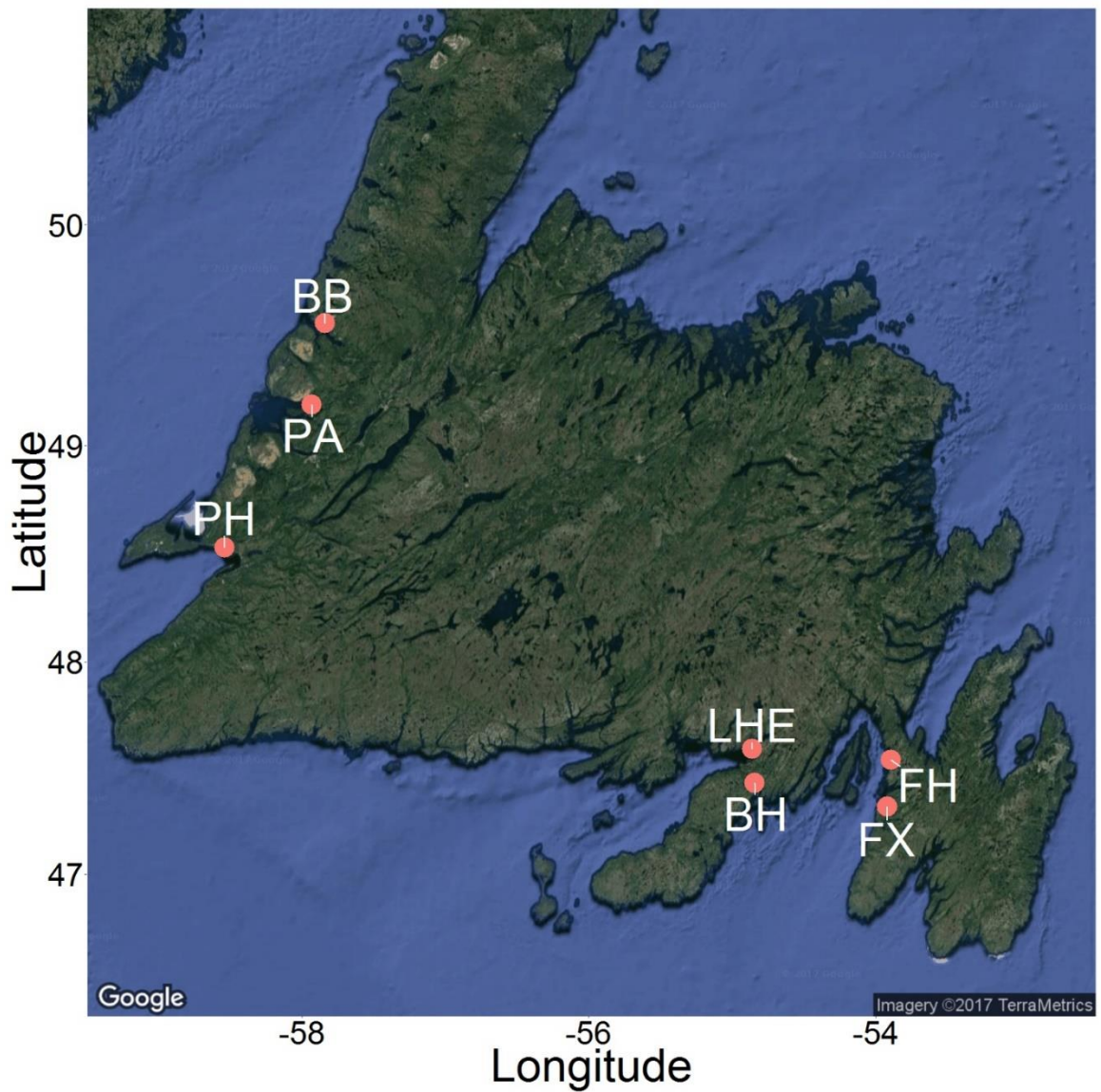


Figure 2.3. Map of 2015 and 2016 study sites across Newfoundland.

Sites included Bonne Bay (BB), Boat Harbour (BH), Fair Haven (FH), Little Harbour East (LHE), Penguin Arm (PA), Little Port Harmon (PH), and Fox Harbour (FX). Map imagery © 2017 TerraMetrics.

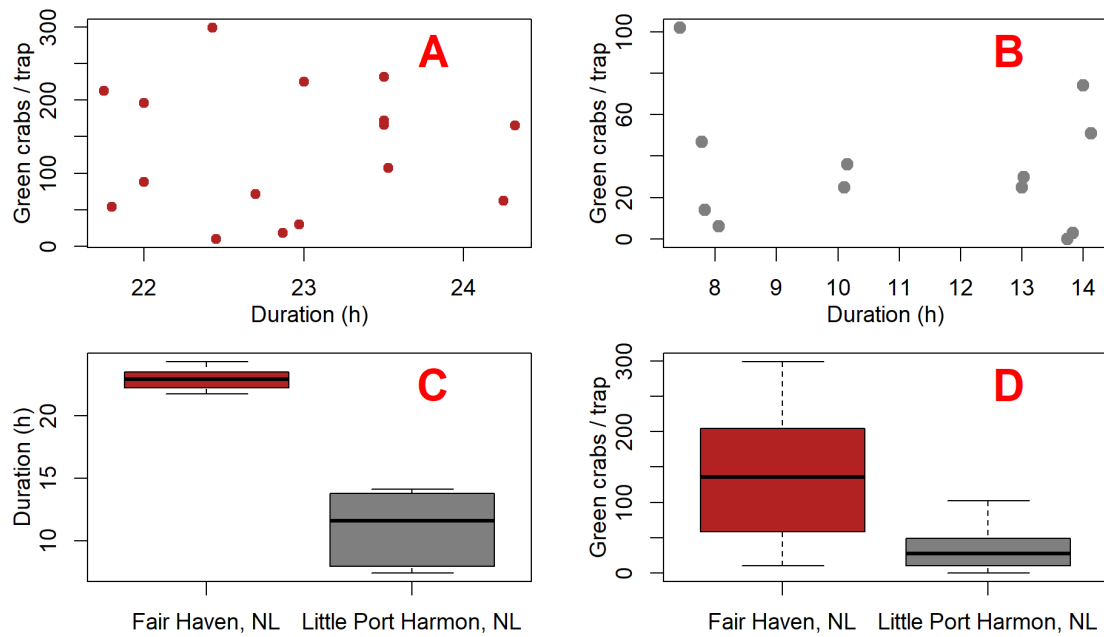


Figure 2.4. Plots comparing green crab catch and fishing duration between Fair Haven, NL and Little Port Harmon, NL.

Scatterplots A and B show the duration and number of green crabs captured for each deployment at Fair Haven (A) ($n = 16$) and Little Port Harmon (B) ($n = 13$), respectively. Boxplot C shows the mean deployment duration at Fair Haven and Little Port Harmon. Boxplot D shows the mean green crab catch per Fukui trap at Fair Haven and Little Port Harmon.

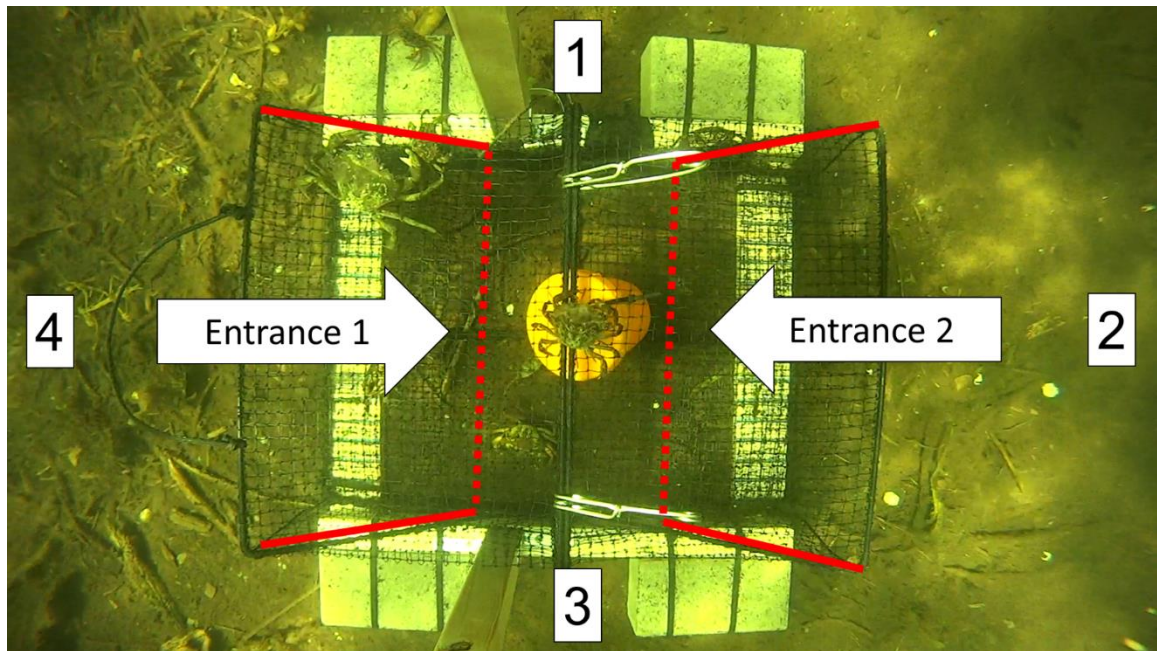


Figure 2.5. A screen shot from a video recording showing the top-down view of a Fukui trap as it actively fishes in situ.

Approaches were recorded every time an animal entered the FOV from direction 1, 2, 3, or 4. The entrance tunnels are outlined with red lines. The dotted red line indicates the entry slits into the trap.

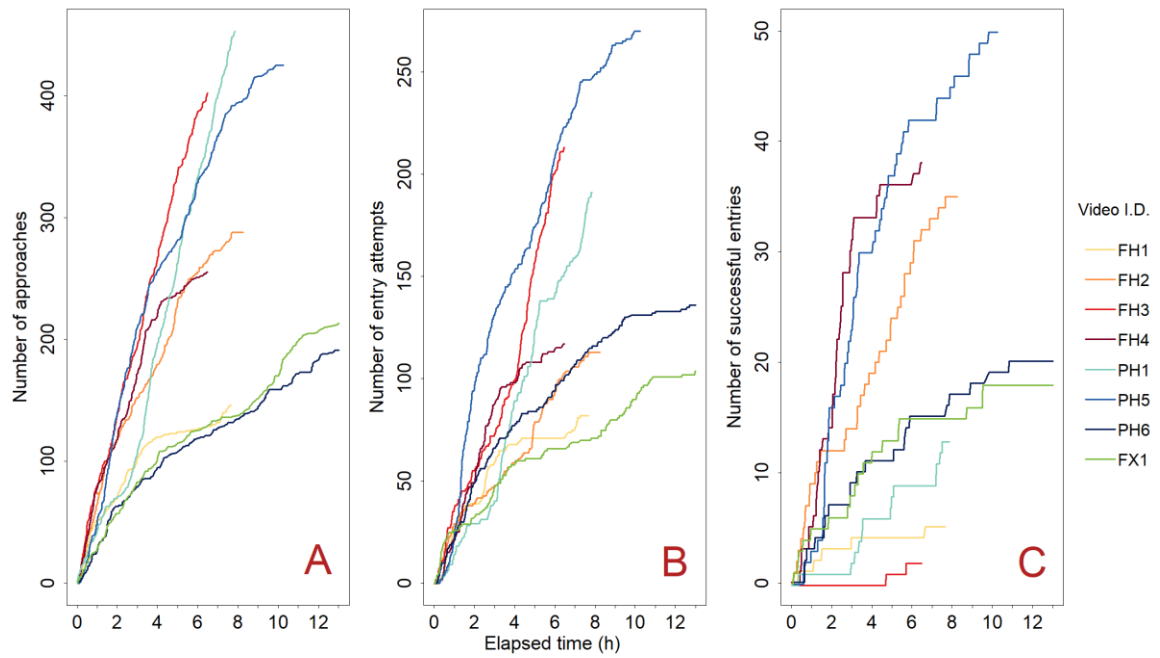


Figure 2.6. Green crab accumulation over the course of each trap deployment ($n = 8$).

Green crab approaches (A), entry attempts (B), and accumulation in the Fukui trap (C).

We did not observe any exits; therefore, panel C represents both the number of successful entries, and the number of green crabs in the trap. Each coloured line (Video ID) represents the individual deployment of a camera-equipped Fukui trap at either Fair Haven (FH) (red-orange colour scheme), Little Port Harmon (PH) (blue colour scheme), or Fox Harbour (FX) (green colour scheme).

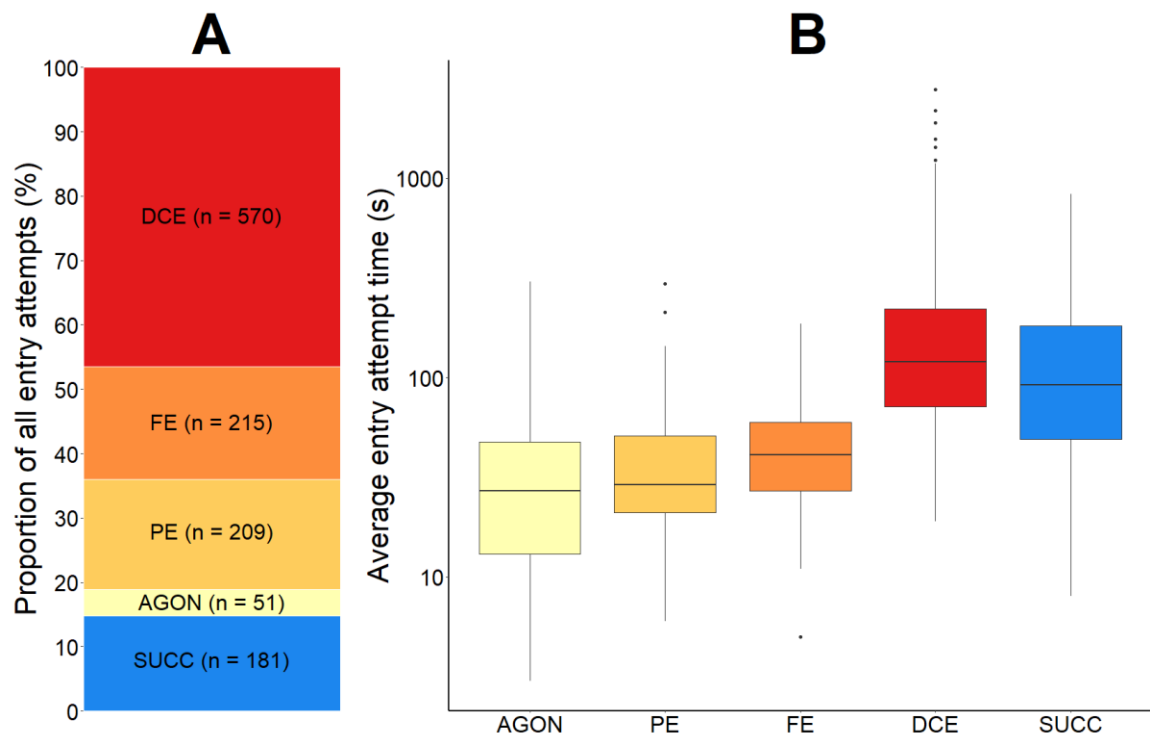
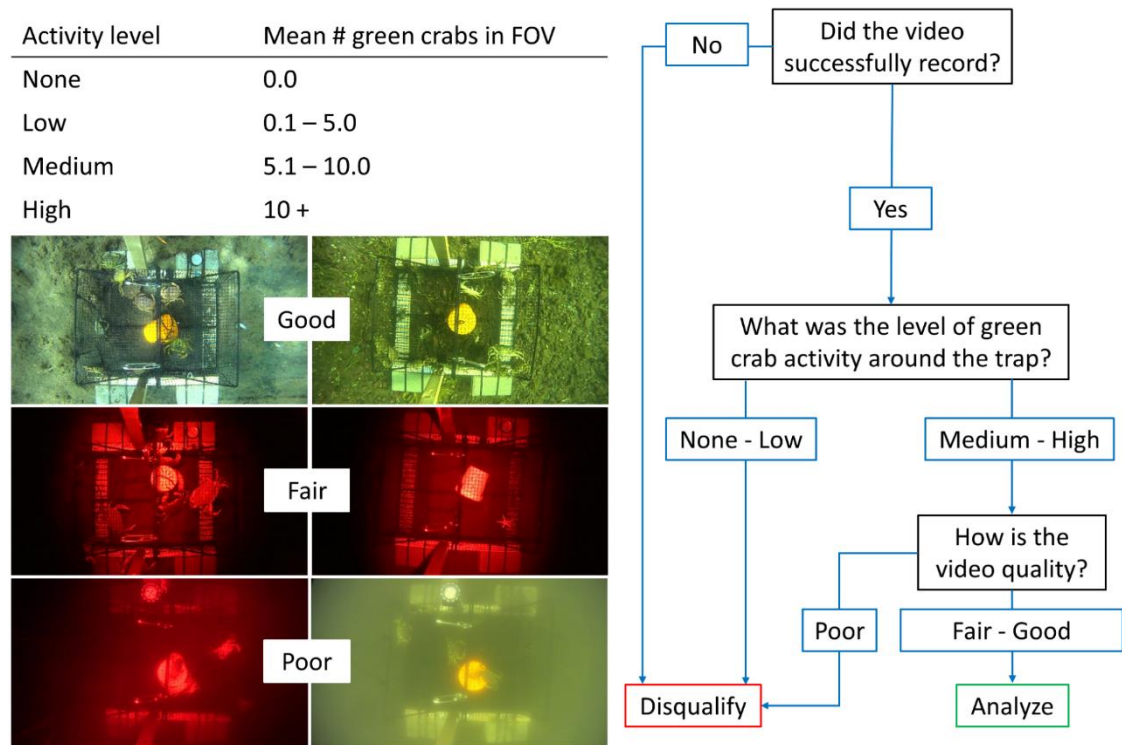


Figure 2.7. The proportional outcome and average time taken for all green crab entry attempts into the Fukui trap.

The proportion of all green crab entry attempts that were successful and that were failures (A). The failed proportion is subdivided according to the four most common reasons for failure: agonistic behaviour (AGON), partial entry (PE), full entry (FE), and difficulty completing entry (DCE). The total number (n) of entry attempts for each is given. A boxplot illustrating the average time (seconds, log scale used) for each type of entry attempt (B). The solid black line within the box depicts the median. The lower and upper hinges of the box correspond to the first and third quartiles, respectively. The upper whisker extends to the largest value no further than 1.5 times the inter-quartile range ($1.5 \times \text{IQR}$). The lower whisker extends to the smallest value no further than $1.5 \times \text{IQR}$. Any data points beyond these whiskers are considered outliers, and are plotted individually.

2.9 Supplementary Figures



Supplementary Figure 2.1. Video selection key used to determine which videos were suitable for analysis.

2.10 Supplementary Information

The raw data collected from our video analysis is available online:

<https://peerj.com/articles/4223/#supp-6>

2.11 Acknowledgements

We thank many individuals for their assistance and contributions to this project. We thank DFO for providing the Fukui traps and bait used in this study. We thank staff at the Marine Institute's Centre for Sustainable Aquatic Resources (Terry Bungay and George Legge) for assistance in constructing and testing the camera apparatus. We acknowledge DFO staff from the Aquatic Invasive Species program and the Ecological Sciences Section (Kyle Matheson, Ashley Bungay, Haley Lambert, Dave Forsey, Rebecca Raymond, and Bob Whalen) for their assistance with fieldwork, as well as DFO Fisheries Patrol Officers (Sherry Pittman and Kim Sheehan) for assistance with fieldwork in the Bay of Islands, NL. We also acknowledge the MUN Field Services team (Andrew Perry, Zach Ryan, and George Bishop) for their assistance in the field. We thank Sheldon Peddle with ACAP Humber Arm for providing us with additional bait, and for delivering replacement camera equipment while in the field. We thank Bob Hooper with the MUN Bonne Bay Marine Station for providing access to a boat, field resources, and accommodation. For fieldwork conducted in Fox Harbour we thank Gerard O'Leary for access to private property for the deployment of our camera equipment. We thank one anonymous reviewer, Leslie Roberson, and our academic editor, Dr. Donald Kramer for their constructive reviews of our manuscript, which greatly enhanced the final paper. Finally, we would like to respectfully acknowledge that we conducted this research on the unceded, unsurrendered ancestral Lands of the Mi'kmaq and Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi'kmaq and Beothuk.

**Chapter 3: Improving the efficiency of the Fukui trap as a capture tool for the
invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada**

3.1 Abstract

The European green crab (*Carcinus maenas*) is a crustacean species native to European and North African coastlines that has become one of the world's most successful marine invasive species. Targeted fishing programs aimed at removing green crabs from invaded ecosystems commonly use Fukui multi-species marine traps. Improving the efficiency of these traps would improve the ability to respond to green crab invasions. In this study, we developed four distinct trap modifications that were designed to facilitate the successful capture of green crabs, with the goal of improving the performance of the Fukui trap. We tested these modifications *in situ* during the summer of 2016 at two locations in Placentia Bay, Newfoundland. We discovered that three of our modified Fukui trap designs caught significantly more green crabs than the standard Fukui trap, increasing catch-per-unit-effort (CPUE) by as much as 81%. We conclude that our top-performing modifications have great potential for widespread use with existing Fukui traps that are being used for green crab removal efforts.

3.2 Introduction

The European green crab, *Carcinus maenas* (Linnaeus, 1758) is a globally successful aquatic invader, now present on every continent with temperate shores (Behrens Yamada, 2001; Roman, 2006; Darling et al., 2008). In Newfoundland, the European green crab (hereafter green crab) was first detected in 2007, and it has since become established across the southern and western coasts of the island (Best, McKenzie & Couturier, 2017). These invasions threaten the native ecosystem through the destruction of sensitive eelgrass beds (Malyshev & Quijón, 2011; Garbary et al., 2014; Matheson et al., 2016), predation on native bivalves (Ropes, 1968; Cohen, Carlton & Fountain, 1995; Matheson & McKenzie, 2014), and competition with native species for food and habitat (Cohen, Carlton & Fountain, 1995; Matheson & Gagnon, 2012).

The complete eradication of an invasive species in a marine environment is virtually impossible once the organism has become established (Bax et al., 2003; Lodge et al., 2006), and may only be possible if the invasion is in a confined area and is addressed shortly after arrival (Culver & M. Kuris, 2000; Simberloff, 2001; Bax et al., 2002). In Newfoundland, the complete eradication of green crabs is no longer considered an option. Therefore, removal efforts have focused on trapping to suppress invasive populations, and to slow further spread (DFO, 2011b). Focused trapping has become the predominant strategy for addressing green crab invasions on both the east and west coasts of Canada (Duncombe & Therriault, 2017; Bergshoeff et al., 2018).

These removal efforts usually use the Fukui multi-species marine trap (model FT-100, Fukui North America, Eganville, Ontario, Canada) to capture green crabs. These

traps are favoured as they are light-weight, collapsible, durable, and can be deployed in large numbers from small boats or from shore. A standard Fukui trap consists of a rectangular, vinyl-coated high tensile steel frame (60 x 45 x 20 cm) covered with square, single-knotted, polyethylene mesh (12 mm bar length). There are two entrances at either end of the trap, where two netting panels form a horizontal “V” with a 45 cm expandable entry slit at the narrow end. To enter the trap through either of these entrances, green crabs must force themselves through the entrance which remains tightly compressed in its default position.

Our previous study was the first formal investigation of the interactions between green crabs and the standard Fukui trap (Bergshoeff et al., 2018). In that study, we mounted underwater video cameras to Fukui traps deployed *in situ* to assess the performance and efficiency of this gear, and to identify design features that were inhibiting green crab entry or facilitating exit prior to gear retrieval (Bergshoeff et al., 2017, 2018). Through these experiments, we discovered that only 16% of the green crabs that attempted to enter the Fukui trap were successfully captured. Our primary finding was that a combination of entanglement in the mesh and the restrictive trap entrance would often inhibit the successful entry of green crabs into the trap (Bergshoeff et al., 2018).

The main objective of this present study was to improve the efficiency of the Fukui trap as a capture tool for green crabs. Based on our video observations from the previous experiment, we developed four distinct modifications designed to facilitate the successful entry of green crabs into Fukui traps. We tested these modified Fukui traps *in*

situ during the summer of 2016 and compared catch-per-unit-effort (CPUE) between each modified trap type and the standard Fukui trap. Our modifications were designed to be simple and practical, so that they could be easily applied to existing Fukui traps that are already in use for green crab removals. Our primary goal was to assess how these novel modifications perform, and to determine their potential for use in green crab removal programs that employ Fukui traps.

3.3 Methods

3.3.1 Modifications

We developed four distinct trap modifications. For the first modification, we attached three 28.3 g (1-oz) lead bass casting sinkers with swivelling brass eyelets to the lower lip of each trap entry slit using 10.2 cm (4") cable ties (Figure 3.1A). The sinkers were evenly spaced along the entry slit, with one in the middle, and two attached 7 cm from the outer edge. The sinkers expanded the size of the trap entrance to approximately 2 cm at its widest point. For the second modification, we attached a 26 x 44 cm panel of black, fibreglass window screen (1 x 1 mm mesh size) to both the top and bottom of each trap entry tunnel (Figure 3.1B). We used braided polyester string (0.825 mm diameter) to stitch these panels on top of the existing mesh. The panels were aligned so that a 4 cm wide strip of mesh extended through the trap entrance, which could be folded under the entry slit lip and stitched in place. For the third modification, we placed a thin strip of fibreglass window screen on the inside of trap, adjacent to the trap entrance, which was designed to aid green crabs in pulling themselves through the restrictive opening (Figure 3.1C). We cut a 4 x 54 cm strip of mesh and folded both ends to create a 42 cm long strip.

The folded, reinforced ends were then attached to the inside wall of the trap using three 10.2 cm (4") cable ties. The edge adjacent to the trap entrance was then loosely attached to the lower lip of the entry slit using three evenly spaced, partially-tightened cable ties. For the forth modification, we used braided polyester string (0.825 mm diameter) to hold the trap entrance open (Figure 3.1D). We used a 21 cm long piece of string to hold the upper and lower half of the entry slit open at the midpoint. The string was passed through either the top or bottom panel of the trap and tied to create a 7 cm loop. Once secured, the string created an oval-shaped opening, and increased the size of the trap entrance to approximately 6 cm at its widest point. For convenience, we named these trap modifications the *sinker*, *mesh*, *assist*, and *string* modifications, respectively, with an unmodified Fukui trap serving as our control.

3.3.2 Fieldwork

We conducted our experiment in Fox Harbour, NL and North Harbour, NL during the summer of 2016 (Figure 3.2). We ran the experiment for 26 days in total at Fox Harbour (June 15-18, June 21-25, June 28-July 5, July 12-16, August 4-12), and 9 days in total at North Harbour (July 18-27). We set traps in fleets of five, which consisted of the four different modified traps (i.e., *sinker*, *mesh*, *assist*, *string*) and an unmodified control trap. These fleets were deployed repeatedly in fixed locations across each study site, which we referred to as 'blocks'. The order of the five traps was randomized within each block. There were three blocks at Fox Harbour (FoxA, FoxB, and FoxC) and three in North Harbour (NorthA, NorthB, and NorthC) (Figure 3.2). These blocks were spread out to provide sampling positions at multiple points within the two bays in which we

conducted the experiment. The specific location of each block was selected based on accessibility by road and the presence of green crabs following a pilot study conducted in early June 2016 (North Harbour: June 2; Fox Harbour: June 8-9).

We baited each trap with approximately 200 g of Atlantic herring (*Clupea harengus*) that was thawed, cut into pieces, and placed in a perforated plastic bait container suspended inside the centre of the trap. Prior to each deployment, each trap was assigned a unique identification number and the order of traps within each fleet was pre-determined using a random sequence generator in R (R Core Team, 2015). We deployed the traps from shore during low tide so that they remained consistently submerged for the duration of the deployment. The traps within each fleet were placed approximately 10 m apart, matching the spacing used in other Fukui trap-based studies (Gillespie et al., 2007; Behrens Yamada & Gillespie, 2008; Curtis et al., 2015; Bergshoeff et al., 2018). Our objective was to deploy each fleet for a 24-hour period, retrieving them at low tide the following day.

Upon retrieval of the traps, we placed all captured green crabs in large polyethylene bags (80 cm x 36 cm) along with a waterproof label indicating the unique identification number assigned to each trap. All bycatch species were visually identified to the lowest possible taxonomic level, recorded, and released as soon as possible. Once the catch was processed, the traps were baited with fresh herring, and re-deployed in a new random sequence. We repeated the entire process across all three blocks. All captured green crabs were euthanized by freezing, and prior to disposal they were counted, sexed, and measured. We measured the carapace width of each green crab using

digital Vernier calipers between the fourth and fifth anterolateral carapace spines (i.e., notch to notch).

This project was approved as a ‘Category A’ study by the Institutional Animal Care Committee at Memorial University of Newfoundland as it involved only invertebrates (project # 15-02-BF), and our field experiment was conducted under experimental license NL-3271-16 issued by Fisheries and Oceans Canada (DFO).

3.3.3 Statistical analysis

3.3.3.1 Total catch vs. trap type

We conducted all analyses and produced all figures using R Statistical Software (R Core Team, 2015). We employed a generalized linear mixed-effects model (GLMM) to test whether the number of green crabs captured per trap differed with trap type, and whether the deployment location (i.e., block) had an influence on total catch. GLMMs are powerful statistical models that can be used to analyze non-normal data that involves random effects (Bolker et al., 2009). Our deployment durations remained consistent from one deployment to the next (mean = 23.9 h; SD = 2.4). Therefore, our CPUE was defined as the total number of green crabs captured per each individual trap deployment. To model catch as a function of the covariates, a negative binomial GLMM with a log link function was used [Eqn. (1)]. We had initially tested a Poisson GLMM, but found it to be overdispersed; therefore, we switched to a negative binomial distribution. The log link function ensured positive fitted values, and the negative binomial distribution was appropriate for our count data. We followed the equation nomenclature and style for presenting statistical models as outlined in Zuur & Ieno, 2016.

The fixed covariates in our model are *trap type* (categorical with five levels: control, sinker, mesh, assist, string), and *block* (categorical with six levels: FoxA, FoxB, FoxC, NorthA, NorthB, NorthC). We had tested for an interaction between *trap type* and *location* (categorical with two levels: Fox Harbour, North Harbour), but found it to be non-significant; therefore, we removed it from our final model. In general, we found green crab distributions to be patchy, with a great deal of local-scale variation within each site. Therefore, *block* was included as a covariate to model the effect of spatial variation between the deployment locations. We deployed 15 traps per day and total catch was not uniform across days; therefore, we included *study day* as a random intercept. This allowed us to incorporate the dependency structure among observations within the same study day, and to account for temporal variations in the environment (e.g., water temperature, weather).

To determine our final model we conducted stepwise backward model simplification, dropping non-significant terms (e.g., *duration*) one at a time until all terms in our model were statistically significant (procedure outlined in Crawley, 2012). Our final model was specified as follows:

$$\begin{aligned}
TotalCatch_{ij} &\sim NB(\mu_{ij}, k) \\
E(TotalCatch_{ij}) &= \mu_{ij} \\
var(TotalCatch_{ij}) &= \mu_{ij} + \mu_{ij}^2/k \\
\log(\mu_{ij}) &= TrapType_{ij} + Block_{ij} + StudyDay_i \\
StudyDay_i &\sim N(0, \sigma^2)
\end{aligned}$$

[Eqn. (1)]

To fit the above model in Eqn. (1), we used the lme4 package (Bates et al., 2017) in R (R Core Team, 2015). We verified the model assumptions by plotting residual versus fitted values, residuals versus covariates in the model, and residuals versus covariates excluded from the model.

3.3.3.2 Carapace width vs. trap type

We constructed a linear mixed-effects model (LME) to test whether the mean carapace width of captured green crabs differed with trap type, and whether there was an interaction between carapace width for male and female green crabs (i.e., sex), and trap type. The carapace width measurements were normally distributed; therefore, we assumed a normal distribution in our model with an identity link [Eqn. (2)].

The fixed covariates in our models were *trap type* (categorical with five levels: control, sinker, mesh, assist, string), *sex* (categorical with two levels: female, male), and *block* (categorical with six levels: FoxA, FoxB, FoxC, NorthA, NorthB, NorthC). *Block* was included in our model to account for any spatial variability between green crab populations in Fox Harbour and North Harbour. We tested for an interaction between *sex* and *trap type*. Finally, we included *study day* as a random intercept to incorporate the dependency among observations of the same study day, and to account for temporal variations. Our final model was specified as follows:

$$CarapaceWidth_{ij} \sim N(\mu_{ij}, \sigma^2)$$

$$E(CarapaceWidth_{ij}) = \mu_{ij}$$

$$var(CarapaceWidth_{ij}) = \sigma^2$$

$$\sigma_{ij} = \text{TrapType}_{ij} + \text{Sex}_{ij} + \text{Block}_{ij} + \text{TrapType}_{ij} \times \text{Sex}_{ij} + \text{StudyDay}_i$$

$$\text{StudyDay}_i \sim N(0, \sigma^2)$$

[Eqn. (2)]

To fit models in Eqn. (2) we used the nlme package (Pinhero et al., 2017) in R (R Core Team, 2015). We verified the model assumptions by plotting residual versus fitted values. The residuals met the assumptions for homogeneity, normality, and independence.

3.4 Results

3.4.1 Fieldwork

We captured a total of 17,615 green crabs across 520 deployments (104 fleets) with an average catch of 34 green crabs per trap (SD = 25.4). We deployed 390 traps (78 fleets) in Fox Harbour, and 130 traps (26 fleets) in North Harbour (Table 3.1). We lost data from a single fleet (NorthA, $n = 5$ traps) in North Harbour on July 23 because the traps were washed ashore during a storm event. Deployment durations ranged from 13.8 to 27.1 h (mean = 23.9 h; SD = 2.4). Short deployment durations can be attributed to the logistical challenges of switching from trap deployments during evening low tide, to morning low tide.

Bycatch for both the standard and modified Fukui traps was minimal (Table 3.2). The most common occurrence of bycatch was rock crab (*Cancer irroratus*) in traps with the *sinker* and *assist* modifications.

3.4.2 Statistical Analysis

3.4.2.1 Total catch vs. trap type

The catch rates associated with the different trap types are summarized in Table 3.3. Fukui traps equipped with the *sinker* (GLMM: $\beta = 0.461$, S.E. = 0.074, $z = 6.220$, $p = 0.000$), *mesh* (GLMM: $\beta = 0.253$, S.E. = 0.075, $z = 3.370$, $p = 0.001$), and *assist* (GLMM: $\beta = 0.593$, S.E. = 0.074, $z = 8.030$, $p = 0.000$) modifications all caught significantly more green crabs than the unmodified control traps (Figure 3.3). The catch rate was not significantly different between traps with the *string* (GLMM: $\beta = 0.029$, S.E. = 0.075, $z = 0.380$, $p = 0.705$) modification and the control traps. There was some variability in catch rates between the different experimental blocks, and the catch rate at FoxA was significantly higher than all other experimental blocks (Supplementary Figure 3.1). During the development of our model we found there was no significant interaction between *trap type* and *location*; therefore, despite spatial variations in catch between blocks, the efficiency of the modified traps is not influenced by the location.

The output of our model is presented in Table 3.4, and the parameter estimates for each modified trap can be explained as follows: First, the *mesh* trap caught 1.29 (95% CI [1.11, 1.49]) times as many green crabs as the control trap which translates to a 29% increase in catch relative to the standard Fukui trap. Second, the *sinker* trap caught 1.59 (95% CI [1.37, 1.83]) times as many green crabs as the control trap which translates to a 59% increase in catch relative to the standard Fukui trap. Third, the *assist* trap caught 1.81 (95% CI [1.57, 2.09]) times as many green crabs as the control trap which translates to an 81% increase in catch relative to the standard Fukui trap. Finally, the *string* trap did

not show any statistically significant improvement over the control trap, catching 1.03 (95% CI [0.89, 1.19]) times as many green crabs. This translates to a 3% increase in total catch relative to the standard Fukui trap.

3.4.2.2 Carapace width vs. trap type

We measured 17,652 green crabs in total (Figure 3.4). Across all trap types, carapace width for male green crabs ranged from 21.1 – 77.0 mm (mean = 52.4 mm; SD = 7.7). For female green crabs, carapace width ranged from 25.4 – 60.8 mm (mean = 41.8 mm; SD = 4.8). Male green crabs were significantly larger than female green crabs by 9.8 mm (LME: $\beta = 9.823$, S.E. = 0.369, $t = 26.636$, $p = 0.000$). For female green crabs, there was no significant difference in carapace width between the modified traps and the unmodified control (Table 3.5). There was a significant interaction between *sex* and *trap type*. Both the *sinker* (LME: $\beta = 1.213$, S.E. = 0.486, $t = 2.494$, $p = 0.013$) and *string* (LME: $\beta = 1.914$, S.E. = 0.531, $t = 3.602$, $p = 0.000$) modifications caught male green crabs that were larger than the male crabs caught in the control traps. All parameter estimates, and the specific results of *block* can be found in Table 3.5. In general, green crabs caught in North Harbour were larger than green crabs caught in Fox Harbour, demonstrating the variability in green crab populations from one location to the next.

3.5 Discussion

3.5.1 Modified trap performance

Modifications made to fishing gear designs can have a considerable impact on catch rates and catch composition. Modifications can be used to promote the switch to

more sustainable fishing gears (Ljungberg et al., 2016; Meintzer, Walsh & Favaro, 2018), reduce the bycatch of non-target species (Broadhurst, 2000; Furevik et al., 2008; Favaro, Duff & Côté, 2013; Serena, Grant & Williams, 2016), improve selectivity for a target species (Moran & Jenke, 1990; Boutson et al., 2009; Ovegård et al., 2011; Winger & Walsh, 2011), and increase the overall catch rate of a fishing gear (Sheaves, 1995; Nguyen et al., 2017; Meintzer, Walsh & Favaro, 2018). In this study, we tested four different modifications designed to improve the efficiency of the Fukui trap as a tool for removing green crabs from invaded ecosystems. These modifications were specifically developed to address the most common inefficiencies in the design of the Fukui trap identified in Bergshoeff et al., 2018 – primarily the entanglement of green crabs in the trap mesh, and the restrictive trap opening that inhibits the successful entry of green crabs into the trap.

Our least effective design was the *string* modification, which did not show any significant improvement in green crab CPUE when compared to the control. We suspect this low CPUE can be attributed to a high frequency of escape events. The *string* modification was designed to expand the trap entrance to approximately 6 cm at its widest point. By contrast, the control trap's entrance remains tightly closed in its default position. This restrictive entrance does not allow green crabs to escape once captured; however, it also makes it harder for crabs to enter the traps (Bergshoeff et al., 2018). A large trap entrance facilitates entry, but can also increase the frequency of escapes, thereby reducing capture efficiency (Archdale et al., 2007). In our design, the strings caused both the upper and lower panels of the entry slit to curve outwards (Figure 3.1D).

We suspect this made it relatively easy for captured green crabs to climb out and escape, nullifying the benefits of a larger trap entrance. Our design could likely be improved by adjusting the length of the strings to create a smaller opening. However, we found the overall design of this modification impractical, as the positioning of the strings made it difficult to clear captured green crabs from the trap once it was retrieved.

We designed the *mesh* modification to facilitate the entry of green crabs into the Fukui trap by preventing their pereopods and anterolateral carapace spines from becoming entangled in the trap mesh during entry attempts (Bergshoeff et al., 2018). We found the *mesh* modification was effective, capturing 29% more green crabs than the standard Fukui trap; however, we suspect that green crabs still encountered difficulty entering the trap. Although the *mesh* modification likely minimized entanglement, the fibreglass window screen panels overlaid on the existing trap mesh appeared to increase the tension of the entry slit. This likely made it more difficult for larger crabs to enter the trap (Figure 3.4). Furthermore, the slippery texture of the window screen may have made it difficult for crabs to gain enough traction to force themselves through the trap entrance. Our modification could likely be improved by replacing the window screen with a proprietary netting material designed for fishing gear. However, we found the process of stitching the mesh panels to the Fukui trap to be time-consuming, which could make adopting this modification impractical for large-scale green crab removal programs.

We designed the *sinker* modification to minimize the difficulty that green crabs experience when attempting to pass through the Fukui trap entrance (Bergshoeff et al., 2018). We found this modification to be simple and effective, producing catch rates that

were 59% greater than the control. Unlike the *string* modification, which was also designed to increase the size of the trap opening, the *sinker* modification did not appear to facilitate frequent escape events. We suspect that the three 28.3 g (1-oz) sinkers expanded the entrance enough for green crabs to navigate through without much difficulty, but not enough that they were able to easily escape once captured, as inferred with the *string* modification. Although it is likely that some green crabs were able to successfully exit the trap, we suspect that most green crabs lacked the maneuverability to make their way back through once inside the trap. In the field, we found the *sinker* modification to be durable, withstanding repeated deployments without requiring any maintenance. Furthermore, unlike the *string* modification, traps equipped with the *sinker* modification were easily emptied upon retrieval. These factors make the *sinker* modification a practical tool for capturing green crabs on a large-scale.

The *assist* modification was designed to aid green crabs in entering the Fukui trap, without increasing the size of the trap entrance. Our previous study revealed that even if a green crab was able to avoid entanglement and reach one of its pereopods or chelipeds through the entrance of a standard Fukui trap, there was nothing for it to grab hold of to pull itself through the opening. This lack of assistance would often result in green crabs failing to successfully enter the trap (Bergshoeff et al., 2018). Through the addition of the *assist* modification, we observed a dramatic 81% increase in the CPUE of the Fukui trap. However, despite the success of this modification in increasing CPUE, our current design would need improvements to make it practical for large-scale green crab removal efforts. Our prototype version lacked the durability required for repetitive usage and often had to

be repaired over the course of our experiment. Like the *mesh* modification, the durability of the *assist* modification could likely be improved by replacing the window screen with a proprietary netting material designed for fishing gear. If the durability of the *assist* modification can be improved this design has the potential to greatly increase the efficiency of green crab removal efforts.

For female green crabs, there was no significant difference in carapace width between our modified traps and the standard Fukui trap. However, for male green crabs, traps equipped with the *sinker* and *string* modifications caught males that were larger than the unmodified control. These two modifications were the only designs where the size of the trap entrance was increased, which would explain their ability to capture larger green crabs. In general, female green crabs are smaller than male green crabs (Best, McKenzie & Couturier, 2017). Therefore, the benefits of a larger entrance in both the *sinker* trap and the *string* trap are only realized by larger male green crabs, which likely experienced greater difficulty entering the *mesh*, *assist*, and control traps, due to the restrictive trap entrance.

Removing large male green crabs from invaded ecosystems will have ecological benefits because reproductive success in males is directly related to size. During the mating season, male green crabs compete aggressively for access to receptive females for mating (Berrill, 1982). The most important factor that determines their success in these conflicts is their size (Reid & Naylor, 1994). These larger males have the reproductive advantage of bigger gonads and more spermatophores, which ultimately enables them to fertilize more eggs, or mate with a larger number of female green crabs (Styrishave,

Rewitz & Andersen, 2004). Additionally, large crabs can forage to deeper depths in the sediment in search of food and can take larger prey (Jensen & Jensen, 1985; Smith, 2004). In general, these larger green crabs will have an advantage over native species when it comes to competition for food (Cohen, Carlton & Fountain, 1995). Therefore, there are ecological benefits to removing the largest crabs from invaded areas, which is encouraged by our *sinker* and *string* modifications. Furthermore, if these modified traps facilitate the capture of larger female green crabs this will have further ecological benefits, as larger females are capable of producing larger egg clutches and have higher reproductive success (Audet et al., 2008; Best, McKenzie & Couturier, 2017).

3.5.2 Bycatch

When compared with fishing gears such as bottom trawls and long lines, traps and pots are advantageous as they are often more selective for species and size, and they promote the live release of bycatch after the gear has been retrieved (Suuronen et al., 2012). Our previous study revealed that bycatch in the Fukui trap is minimal, and that most non-target species could be released unharmed upon retrieval of the trap (Bergshoeff et al., 2018). When used to target green crab, native crustacean species are the most common form of bycatch when using the Fukui trap (Gillespie et al., 2007; Bergshoeff et al., 2018). Modifications are often made to traps with the goal of reducing the bycatch of non-target species, while maintaining the effectiveness of the gear at capturing target species (Zhou & Shirley, 1997; Favaro, Duff & Côté, 2013; Serena, Grant & Williams, 2016).

The goal of our design modifications was to increase the overall capture efficiency of the Fukui trap; therefore, there was a risk that the modified traps would also increase the bycatch of non-target species. Fortunately, bycatch was minimal for all trap types, and mostly limited to native rock crabs (Table 3.2). Rock crabs were most commonly captured in traps equipped with the *sinker* and *assist* modifications. This is not surprising, as these traps were also the most effective at capturing green crabs. Our modifications were designed to facilitate the entry of green crabs into the Fukui trap; therefore, it makes sense that these modifications would also facilitate the entry of other crab species (i.e., rock crab). In both this study and our previous study, we did not observe any predation or mortality of rock crab bycatch (Bergshoeff et al., 2018). Overall, bycatch when using our modified Fukui traps is of minimal concern.

3.5.3 Practical application

We designed our trap modifications to be simple and practical, so that they could be applied to Fukui traps with minimal effort. Overall, based on durability and performance, we conclude that the *sinker* modification is an excellent option for improving the efficiency of the Fukui trap as a selective green crab capture tool. The *assist* modification demonstrated impressive performance; however, durability was an issue which currently limits its practicality for large-scale use. If these durability challenges are addressed, then this modification would be the most effective way to increase green crab CPUE within removal programs. However, the *sinker* modification has the added advantage of catching larger male green crabs. For both male and female green crabs, larger body size is associated with greater reproductive success and

fecundity (Kelley et al., 2015). It has been shown that continuous trapping and the removal of larger crabs from an invaded area can cause a demographic shift towards a younger population, with reduced body mass and reproductive potential (Duncombe & Therriault, 2017). Furthermore, a reduction in the average carapace width of green crabs can cause a shift in their ecological role, from primary predators to potential prey for native crustaceans and shorebirds (DFO, 2011a). Therefore, even though the increase in average carapace width for the *sinker* modification is small, it could provide an advantage to green crab removal programs over time.

In this study, we chose to individually address the common inefficiencies of the Fukui trap; however, to further improve the trap's efficiency it may be possible to combine multiple design modifications into a single modified trap. For example, a Fukui trap equipped with the *sinker* and *mesh* modification would address both the restrictive trap entrance, and the issue of entanglement in the mesh. In addition to trap design modifications, future studies could investigate improved techniques for attracting green crabs to the trap itself. The use of white and purple LED lights has been shown to significantly improve the catchability of snow crab (*Chionoecetes opilio*) traps (Nguyen et al., 2017). Similarly, it may be possible to increase the CPUE of Fukui traps using artificial lighting to attract green crabs. Furthermore, the type of bait used to attract a target species can also have an impact on CPUE (Miller, 1990; Woll et al., 2001; Beecher & Romaine, 2010; Vazquez Archdale & Kawamura, 2011). For green crab, it has been shown that Atlantic cod (*Gadus morhua*) and short-fin squid (*Illex illecebrosus*) can produce green crab catch rates that are statistically greater than Atlantic herring (Butt,

2017). When combined, these techniques could further increase the efficiency of the Fukui trap as a green crab capture tool.

Moving forward, it is essential that ongoing green crab removal programs continue to embed gear design studies within them. It would be a missed opportunity to incorporate the top performing modifications that we tested in this study into green crab removal efforts without further replicating the results against additional control traps. By replicating the results, it would be possible to quantify the benefits of making a switch to modified traps. When testing new modified Fukui traps, a portion of the traps that are being fished should always be devoted to controlled experiments to refine these modifications, until incremental innovation is no longer yielding benefits. For example, our *sinker* modification demonstrated a 59% increase in green crab CPUE; however, incremental innovations to this design (e.g., using both lighter and heavier sinkers) could pinpoint the optimal design that maximizes CPUE and green crab capture efficiency. Furthermore, by incorporating small-scale gear design studies within green crab management programs we can begin to build a culture around making invasive species fishing gear as efficient and effective as possible.

3.6 Conclusion

In summary, this study demonstrates that dramatic improvements in the performance of the Fukui trap can be achieved through simple design modifications. Due to the widespread use and versatility of the Fukui trap as a green crab removal tool, it was important that these modifications were simple, durable, and effective. We conclude that the *sinker* modification meets all these requirements, and that existing Fukui traps can be

easily retrofitted with this design for use on a large-scale. The *assist* modification is also an excellent choice for improving green crab CPUE; however, this design needs durability improvements before it is suitable for use in large-scale green crab removal programs. This emphasises the importance of embedding gear design experiments into ongoing green crab removal efforts. In doing so, incremental improvements can be made to determine the optimal gear design for improving green crab CPUE with Fukui traps. Intensive trapping using the standard Fukui trap has already proven to be an effective technique for reducing green crab populations (Gillespie et al., 2007; DFO, 2011a,b). Therefore, we hope that our recommended design modifications will be adopted and refined by green crab removal programs as an efficient and selective tool to further reduce green crab populations in invaded ecosystems.

3.7 Tables

Table 3.1. Summary of trap deployments at Fox Harbour, NL and North Harbour, NL.

	Traps deployed (n)	Replicates (n)	Deployment duration (h) (mean \pm SD)	Catch per deployment (mean \pm SD)	Min. catch	Max. catch	Total green crabs caught
Fox Harbour	390	78	24.1 \pm 2.2	35.5 \pm 27.6	0	211	13,855
North Harbour	130	26	23.2 \pm 2.8	28.9 \pm 16.8	1	88	3,760
Overall	520	104	23.9 \pm 2.4	33.9 \pm 25.4	0	211	17,615

Table 3.2. Summary of all bycatch species captured in each trap type.

The number of green crabs caught in each trap type has also been included for comparison purposes.

	Control	Sinker	Mesh	Assist	String
Rock crab (<i>Cancer irroratus</i>)	18	42	26	38	33
Sculpin spp. (<i>Myoxocephalus</i> spp.)	1	1	1	0	1
Cunner (<i>Tautogolabrus adspersus</i>)	0	1	1	1	1
Rock gunnel (<i>Pholis gunnellus</i>)	1	0	0	0	2
Atlantic cod (<i>Gadus morhua</i>)	1	0	1	1	0
Winter flounder (<i>Pseudopleuronectes americanus</i>)	0	0	0	0	2
Sea trout (<i>Salmo trutta</i>)	1	0	0	0	0
Green crab (<i>Carcinus maenas</i>)	2,738	4,023	3,529	4,778	2,547

Table 3.3. Summary of green crab captured in each trap type.

Trap type	Traps deployed (<i>n</i>)	Catch per deployment (mean \pm SD)	Minimum catch per deployment	Maximum catch per deployment	Total green crabs captured
Control	104	26.3 \pm 22.0	1	143	2,738
Sinker	104	38.7 \pm 20.7	6	172	4,023
Mesh	104	33.9 \pm 30.7	0	167	3,529
Assist	104	45.9 \pm 30.7	4	211	4,778
String	104	24.5 \pm 12.0	2	61	2,547

Table 3.4. Estimated regression parameters, standard errors, z-values, and P-values for the negative binomial generalized linear mixed-effects model (GLMM) presented in Eqn (1).

The estimated value of σ_{StudyDay} is 0.368.

	Estimate	Std. error	z value	P-value
Intercept	3.456	0.098	35.120	0.000
Sinker	0.461	0.074	6.220	0.000
Mesh	0.253	0.075	3.370	0.001
Assist	0.593	0.074	8.030	0.000
String	0.029	0.075	0.380	0.705
FoxB	-0.323	0.066	-4.920	0.000
FoxC	-0.568	0.067	-8.530	0.000
NorthA	-0.527	0.173	-3.050	0.002
NorthB	-0.379	0.169	-2.240	0.025
NorthC	-0.333	0.169	-1.970	0.048

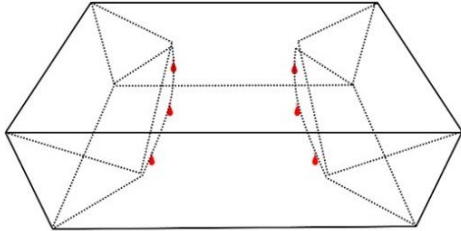
Table 3.5. Estimated regression parameters, standard errors, t-values, and P-values for the linear mixed-effects model (LME) presented in Eqn (2).

The estimated value of σ_{StudyDay} is 1.223.

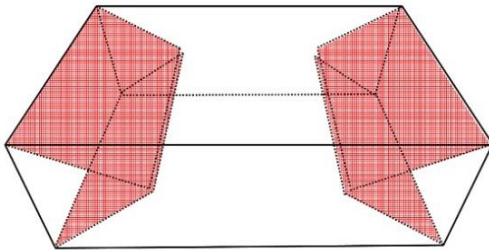
	Value	Std. error	<i>df</i>	<i>t</i> value	<i>P</i> -value
Intercept	40.945	0.423	17549	96.820	0.000
Sinker	0.464	0.447	17549	1.039	0.299
Mesh	-0.565	0.432	17549	-1.308	0.191
Assist	0.253	0.426	17549	0.593	0.553
String	-0.058	0.487	17549	-0.119	0.905
Male	9.823	0.369	17549	26.636	0.000
FoxB	0.614	0.144	17549	4.273	0.000
FoxC	1.695	0.154	17549	11.004	0.000
NorthA	2.988	0.536	17549	5.580	0.000
NorthB	2.190	0.521	17549	4.207	0.000
NorthC	1.987	0.518	17549	3.833	0.000
Sinker:Male	1.213	0.486	17549	2.494	0.013
Mesh:Male	-0.628	0.475	17549	-1.322	0.186
Assist:Male	-0.300	0.464	17549	-0.646	0.518
String:Male	1.914	0.531	17549	3.602	0.000

3.8 Figures

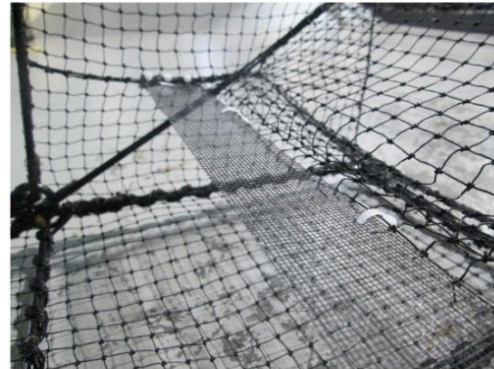
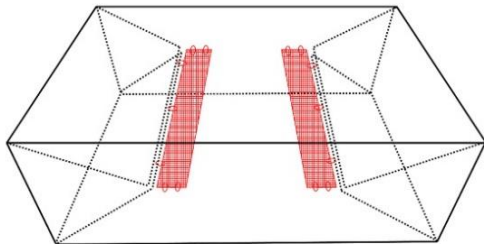
A) Sinker



B) Mesh



C) Assist



D) String

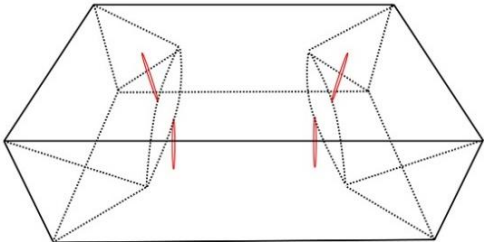


Figure 3.1. The four different trap modifications: sinker (A), mesh (B), assist (C), string (D).

The red coloured objects in each Fukui trap schematic indicate the modification features.

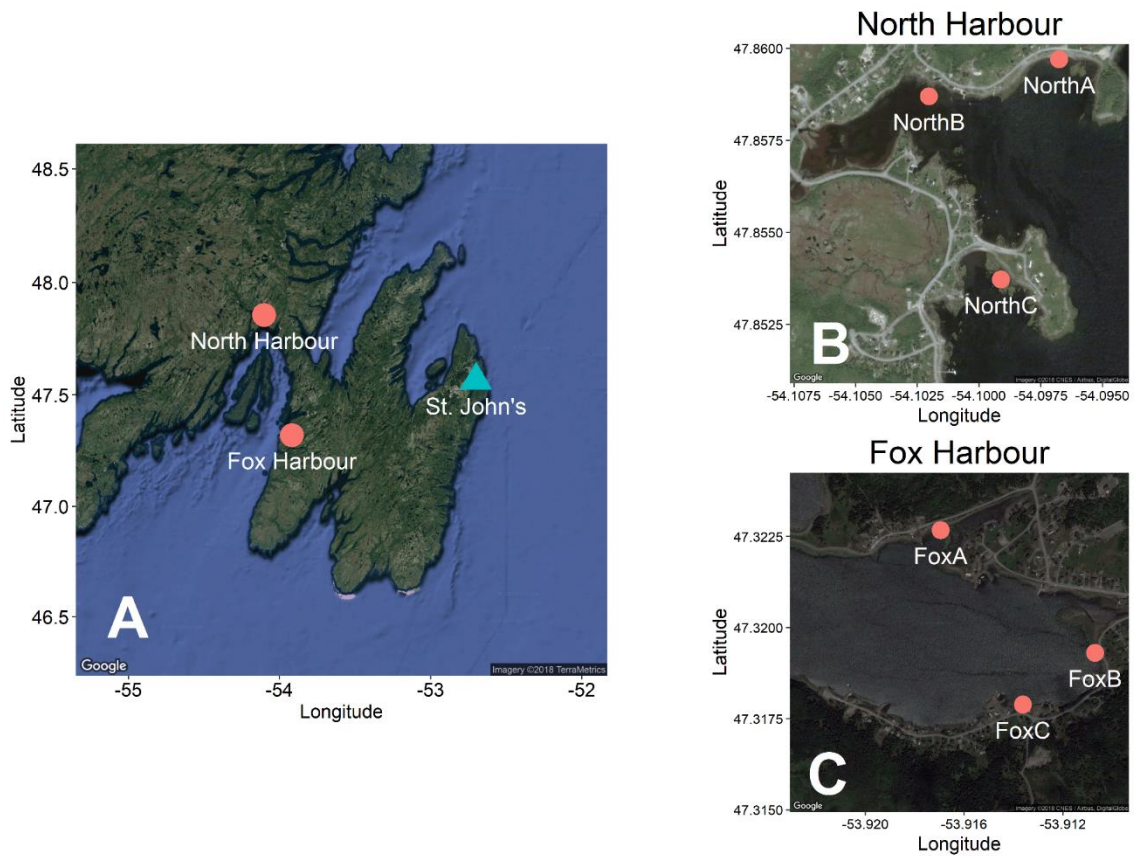


Figure 3.2. Maps showing the location of our study sites and experimental blocks.

Map A shows the location of North Harbour, NL and Fox Harbour, NL. The city of St. John's, NL is included for reference. Map B and C show the location of our experimental blocks at North Harbour and Fox Harbour, respectively. We produced these maps using the ggmap package (Kahle & Wickham, 2013) in R (R Core Team, 2015). Map A imagery © 2018 TerraMetrics. Map B and C imagery © 2018 CNES/Airbus, DigitalGlobe.

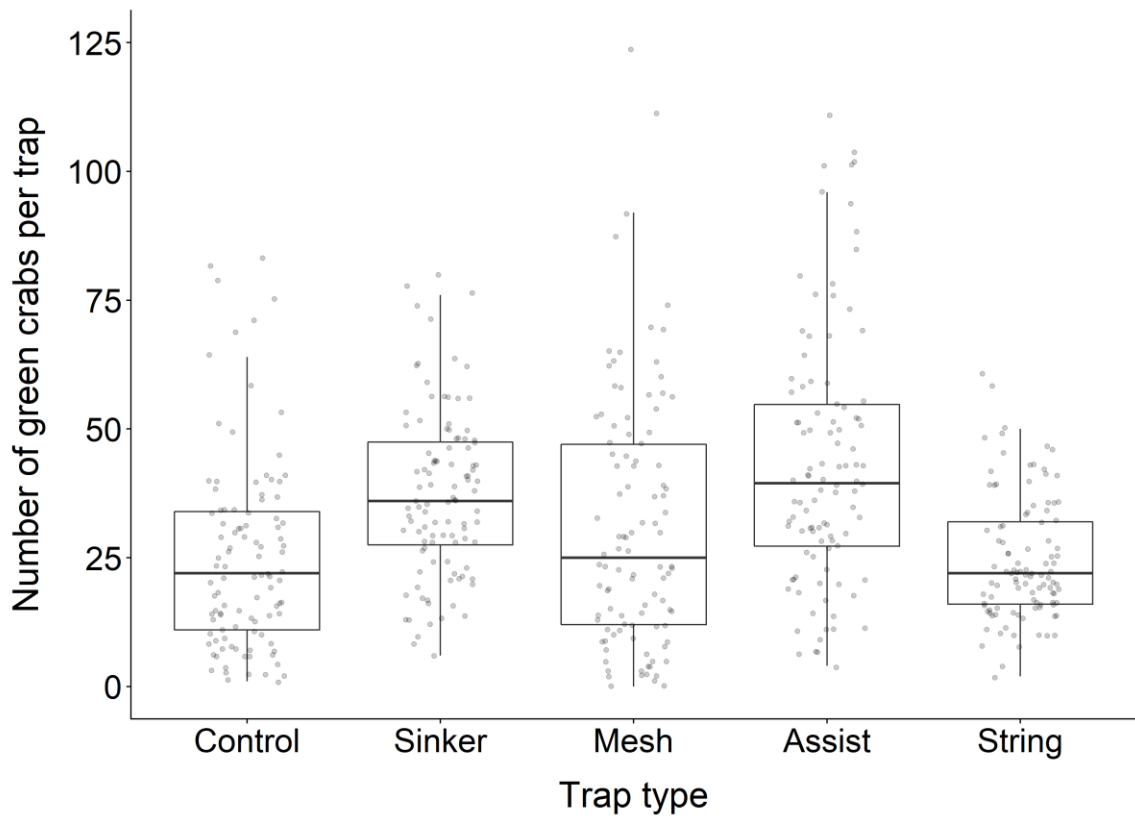


Figure 3.3. Boxplot illustrating the average number of green crabs captured in each trap type.

Each data point represents the number of green crabs captured for an individual trap deployment. The solid black line within each box depicts the median for that trap type. The lower and upper hinges of the box correspond to the first and third quartiles, respectively. The upper whisker extends to the largest value no further than 1.5 times the inter-quartile range ($1.5 \times \text{IQR}$), and the lower whisker extends to the smallest value no further than $1.5 \times \text{IQR}$. Any data points beyond these whiskers are considered outliers. Outliers above 125 are not displayed ($n = 1, 1, 2, 2, 0$ respectively).

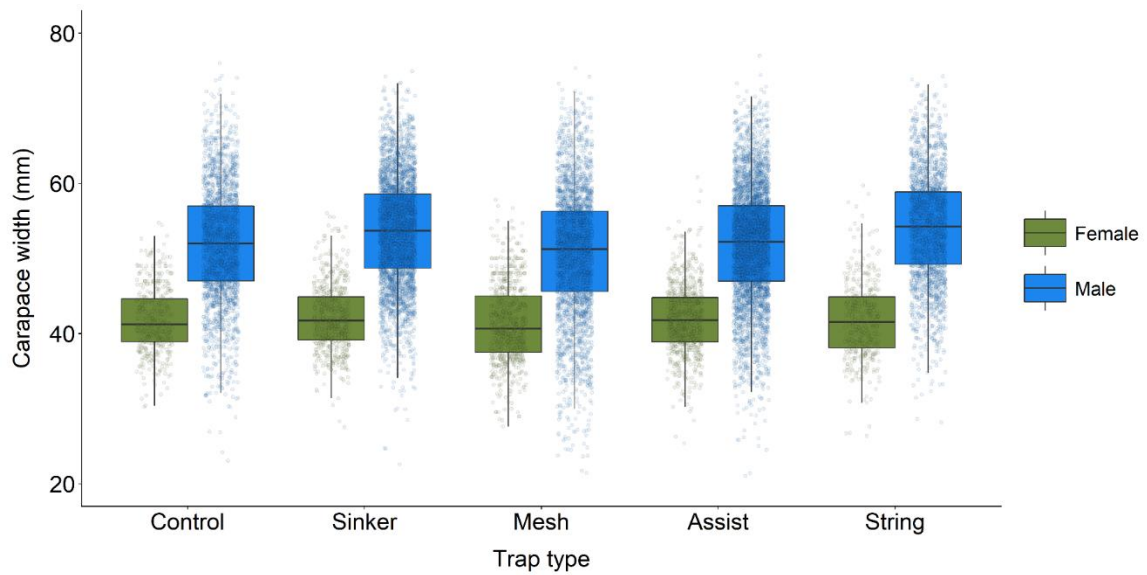
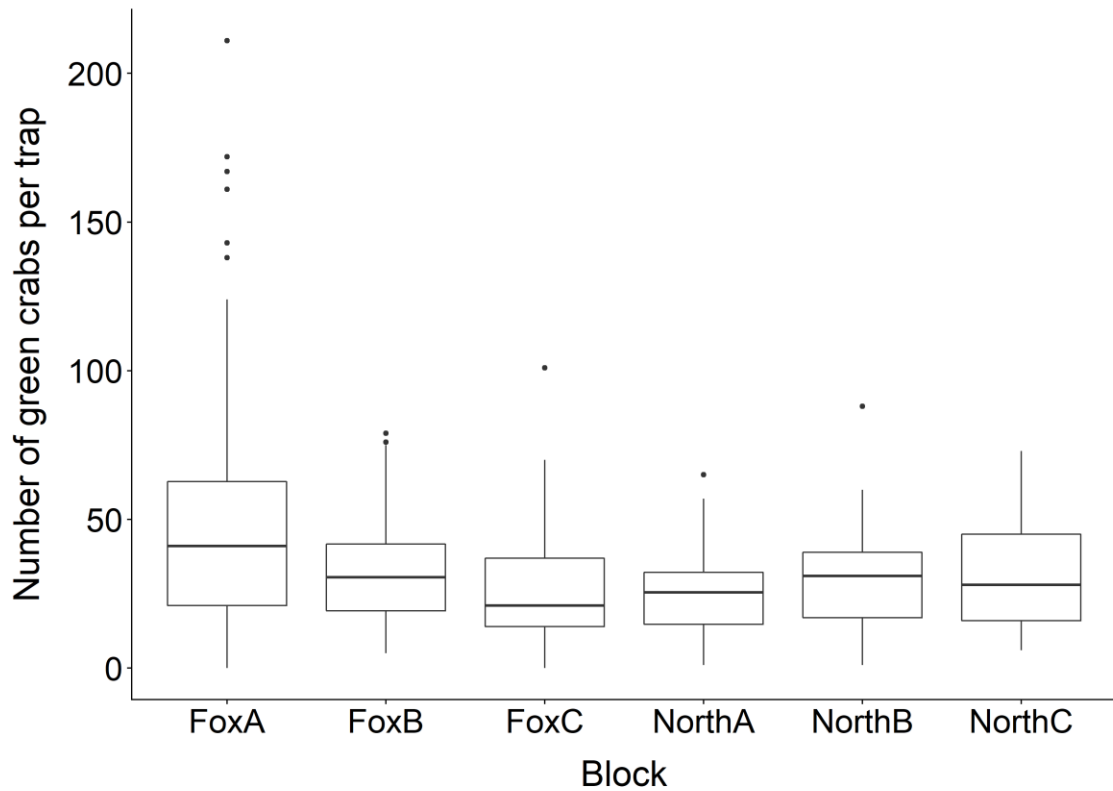


Figure 3.4. A boxplot illustrating the average carapace width of green crabs captured in each trap type.

Each data point represents the carapace width of an individual green crab. The solid black line within each box depicts the median for that trap type. The lower and upper hinges of the box correspond to the first and third quartiles, respectively. The upper whisker extends to the largest value no further than 1.5 times the inter-quartile range ($1.5 \times \text{IQR}$), and the lower whisker extends to the smallest value no further than $1.5 \times \text{IQR}$. Any data points beyond these whiskers are considered outliers.

3.9 Supplementary Figures



Supplementary Figure 3.1. A boxplot illustrating the average number of green crabs captured at each block.

The solid black line within each box depicts the median for that trap type. The lower and upper hinges of the box correspond to the first and third quartiles, respectively. The upper whisker extends to the largest value no further than 1.5 times the inter-quartile range ($1.5 \times \text{IQR}$), and the lower whisker extends to the smallest value no further than $1.5 \times \text{IQR}$.

3.10 Acknowledgments

We would like to thank all individuals who contributed to this project and are especially grateful to Mary Alliston Butt for her assistance with fieldwork. We also thank Maggie Folkins for her assistance in the field. We thank DFO for providing the Fukui traps that were used in this study. We thank Fox Harbour residents, Bob Buckmaster and Gerard O’Leary for access to private property and for their genuine interest in this research. This project was funded by the Marine Environmental Observation Prediction and Response (MEOPAR) Early-Career Faculty Development Grant awarded to Brett Favaro (EC1-BF-MUN). Jonathan A. Bergshoeff was supported by an Ocean Industry Student Research Award from the Research and Development Corporation of Newfoundland and Labrador (5404-1915-101). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Finally, we would like to respectfully acknowledge that we conducted this research on the unceded, unsurrendered ancestral Lands of the Mi’kmaq and Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi’kmaq and Beothuk.

Chapter 4: Summary

The research described in this thesis represents the first formal investigation into the performance and efficiency of the Fukui trap as a capture tool for removing green crabs from invaded ecosystems. Using underwater video to evaluate the interactions between green crabs and the Fukui trap was a novel approach that provided valuable insights into the efficiency of this gear, revealing information that could not be attained from catch data alone. The knowledge gained through this research is critical for invasive species managers that use the Fukui trap for green crab removals and will allow them to respond more effectively to green crab invasions.

Chapter 2 of this thesis demonstrated that although Fukui traps can be used to capture green crabs, there is great potential to improve the overall performance and efficiency of this gear. Analysis of the underwater videos collected in this initial experiment revealed that the rate of successful entry of green crabs into the Fukui trap was low, at only 16%, with the number of failed entry attempts greatly outnumbering successful captures. However, the high number of failed entry attempts were frequently caused by several reoccurring scenarios associated with the design of the trap. Based on these observations, it was clear that simple modifications could be made to the design of the Fukui trap to increase the successful capture of green crabs. Furthermore, the underlying design flaws that contributed to the high frequency of entry attempt failures occurred across all study areas. This demonstrates that the performance of the Fukui trap is not based on region or local green crab behaviour, but rather on gear design. Therefore,

improvements to the design of the Fukui trap will benefit green crab removal efforts wherever these traps are being used.

Chapter 3 of this thesis confirmed that substantial improvements in the performance of the Fukui trap can be achieved through simple design modifications. When tested *in situ*, these modifications improved green crab catch rates by as much as 81%. Although there are alternative fishing gears that can be used to effectively capture green crabs, this study demonstrates that modified Fukui traps remain a viable option for green crab removals. The widespread use and versatility of the Fukui trap necessitates that these modifications be simple, durable, and effective, so that they can be easily applied to traps already being used by invasive species managers to remove green crabs. The *sinker* and *assist* modifications proved to be highly effective, improving green crab catch rates by 59% and 81% respectively compared with the standard Fukui trap. Therefore, adoption of these gear design improvements will greatly benefit green crab removal programs and will act as another tool for reducing and managing green crab populations in invaded ecosystems.

Moving forward, as gear modification research involving the Fukui trap continues, it will be beneficial to once again use underwater video cameras to assess these modifications. Chapter 3 demonstrated that an extensive field-based experiment with many replicates can be used to reliably determine the effectiveness of gear modifications. However, despite the labour-intensive nature of video analysis, the use of underwater video cameras may ultimately be a faster and more accurate means of evaluating the performance of a modified trap. Direct observation of the traps via

recorded videos requires less replicates and can reveal specific issues that would otherwise be undetected by a trapping experiment alone. If green crabs can be directly observed as they interact with modified Fukui traps this will remove the need to make inferences about the performance of the modification based on catch data alone.

Furthermore, although it was not detected by the study presented in chapter 3, it is worth considering whether the performance of the modified Fukui traps would vary depending on green crab density in the area being fished. In certain high-density situations, it may be of little added benefit to implement design modifications if a standard (i.e., not modified) Fukui trap can produce high catch rates. If green crab densities are high, there is the possibility that the trap will become saturated. When a trap becomes saturated, catch rates will decrease as total catch increases. This can be attributed to either the physical limitations of the trap, or agonistic behaviour preventing additional crabs from entering the trap (Miller, 1978). Therefore, the efficiency of a saturated trap is limited to the frequency at which the trap can be retrieved. Conversely, if green crab densities are low, then modifying the Fukui trap is essential to achieve the highest possible catch-per-unit-effort (CPUE). Regardless of population densities, it is beneficial to catch as many green crabs as possible. Overall, the modest modifications presented in this thesis demonstrate inexpensive, yet highly effective options for increasing the CPUE of the Fukui trap, and there is a strong case to implement them in removal programs.

This thesis examined how modifications can be used to improve the efficiency of the Fukui trap; however, gear design is not the only means of improving the efficiency of

removal efforts. In addition to further trap modification experiments, efficiency can also be achieved in the form of costs, time, and fishing effort. To maximize the efficiency of removal efforts using the Fukui trap it may be necessary to focus on how this gear is currently being used to fish for green crabs. CPUE may be further increased by identifying the ideal soak time and retrieval interval that allows the Fukui trap to capture as many green crabs as possible. For example, instead of a single deployment in one 24-hour period, a more efficient Fukui trap may benefit from two 12-hour deployments to maximize the capture of green crabs. This has been demonstrated as an effective fishing strategy for American lobster (*Homarus americanus*), where traps that were emptied twice per day had a greater CPUE than traps emptied only once in a 24-hour period (Miller & Rodger, 1996). Similarly, Miller (1979) observed that traps used to target red rock crabs (*Cancer productus*) over a 12-hour period would achieve a higher cumulative catch if the crabs were removed every two hours, instead of being left untouched for the duration of the deployment.

Although logistically challenging for large-scale removal efforts, use of an improved Fukui trap, in combination with shorter deployment intervals, could be an effective strategy for suppressing green crab populations in invaded areas. However, there are inherent trade-offs between maximizing catch through ideal soak durations and the resources (e.g., equipment, wages, travel) required to deploy these traps – factors that must be considered when determining the most effective removal strategy. Alternatively, based on observations from this thesis, it is possible that total catch would continue to increase beyond a 24-hour deployment period until the traps become completely

saturated. This may still be a viable option to promote efficient removals if resources and logistics prohibit soak times of 24-hours or less. Moving forward, a cost-benefit analysis comparing the total number of green crabs removed versus the resources put in to catching those crabs would be an informative tool for making decisions on how to structure removal programs most efficiently.

As described in this thesis, conducting a baseline investigation into the performance of the Fukui trap and improving the efficiency of this gear through modification, are essential steps towards managing green crab invasions. This knowledge is extremely valuable for addressing and reducing invasive green crab populations; however, there are still critical knowledge gaps that remain surrounding green crab removal efforts, and to what extent these reductions in green crab abundance become ecologically significant (DFO, 2011a). Research has shown that green crabs have a major impact on biodiversity and habitat in invaded area, but the critical number of green crabs per area that causes ecological damage (e.g., destruction of eelgrass beds) is an important factor that remains uncertain (Klassen & Locke, 2007; DFO, 2011a).

Furthermore, intense trapping serves as an important strategy for managing green crab invasions; however, there have been no specific targets established for green crab removals, and the threshold at which green crabs have an impact on invaded ecosystems remains unknown (DFO, 2011b,a). Understanding the threshold of effect that green crabs have on an ecosystem is critical in order to develop sustainable, long-term mitigation efforts, such as restoring damaged eelgrass habitat. Therefore, Fisheries and Oceans Canada (DFO) has recommended further research on determining accurate population

density estimates for green crabs, establishment of critical threshold levels for invaded ecosystems, and more accurate measures of mitigation success based on specific environmental conditions (Cynthia H. McKenzie, pers. comm.).

Green crab invasions preclude complete eradication; therefore, invasive species managers also need to consider how green crab removal efforts can be sustained in the long-term to prevent suppressed populations from rebounding (Pasko & Goldberg, 2014). One potential option for sustained control is to establish a commercial fishery for green crabs. In 2014, DFO introduced a commercial licensed fishery for green crabs in Nova Scotia, followed by several other experimental licenses in the Atlantic region (St-Hilaire et al., 2016; Vercaemer & Sephton, 2016). These commercialized fisheries can be a sustainable method of green crab control; however, a lack of product demand and minimal financial incentives can limit their success (St-Hilaire et al., 2016). The current market for green crabs in Canada is mostly limited to lobster bait; however, with further market development and research there is potential to use green crabs as a food product in Canada (St-Hilaire et al., 2016). Although investigation is still needed, commercial green crab fisheries in Canada may offer a sustainable, long-term solution for controlling green crab populations in invaded coastal ecosystems.

Overall, targeted fishing remains an essential strategy for capturing invasive green crabs, and there are tremendous benefits in reducing green crab abundance in invaded areas (DFO, 2011a; Duncombe & Therriault, 2017). The results presented in this thesis demonstrate that the Fukui trap has great potential as a removal tool for green crabs in invaded ecosystems, and this research adds to the knowledge base that can be drawn

upon to address green crab invasions. A thorough understanding of the performance of the Fukui trap provides greater insight into the impact of removal efforts. Moving forward, it is crucial that research continues towards filling the knowledge gaps surrounding removal targets and critical thresholds for green crabs. Once these targets are determined, the modified Fukui traps can be used as fast and effective tools for drawing down the density of green crabs in invaded ecosystems. Ultimately, this will help to reduce green crab populations, with the goal of preserving the function, diversity, and integrity of native ecosystems.

References:

- Archdale MV., Añasco CP., Kawamura Y., Tomiki S. 2007. Effect of two collapsible pot designs on escape rate and behavior of the invasive swimming crabs *Charybdis japonica* and *Portunus pelagicus*. *Fisheries Research* 85:202–209. DOI: 10.1016/j.fishres.2007.02.008.
- Archdale MV., Kariyazono L., Añasco CP. 2006. The effect of two pot types on entrance rate and entrance behavior of the invasive Japanese swimming crab *Charybdis japonica*. *Fisheries Research* 77:271–274. DOI: 10.1016/j.fishres.2005.11.012.
- Audet D., Miron G., Moriyasu M., Audet Dominique; Miron GMM. 2008. Biological characteristics of a newly established green crab (*Carcinus maenas*) population in the southern Gulf of St. Lawrence, Canada. *Journal of Shellfish Research* 27:427–441. DOI: 10.2983/0730-8000(2008)27[427:bcoane]2.0.co;2.
- Bacheler NM., Schobernd ZH., Berrane DJ., Schobernd CM., Mitchell WA., Geraldini NR. 2013a. When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass (*Centropristis striata*). *ICES Journal of Marine Science* 70:873–882. DOI: 10.1093/icesjms/fst176.
- Bacheler NM., Schobernd CM., Schobernd ZH., Mitchell WA., Berrane DJ., Kellison GT., Reichert MJM. 2013b. Comparison of trap and underwater video gears for indexing reef fish presence and abundance in the southeast United States. *Fisheries Research* 143:81–88. DOI: 10.1016/j.fishres.2013.01.013.

- Barber JS., Cobb JS. 2009. Qualitative observations of Dungeness crabs, *Cancer magister*, in and around traps: evidence of resource guarding and clustering. *Marine and Freshwater Behaviour and Physiology* 42:135–146. DOI: 10.1080/10236240902860011.
- Bates D., Mächler M., Bolker B., Walker S., Christensen RHB., Singmann H., Dai B., Grothendieck G., Green P. 2017. Package “lme4”. R package version 1.1-13, <https://github.com/lme4/lme4/>.
- Bax NJ., Hayes K., Marshall A., Parry D., Thresher R. 2002. Man-made marinas as sheltered islands for alien marine organisms: Establishment and eradication of an alien invasive marine species. In: Veitch CR, Clout NM eds. *Turning the tide: the eradication of invasive species*. Gland, Switzerland: IUCN SSC Invasive Species Specialist Group, 26–39. DOI: 10.1366/0003702991946064.
- Bax N., Williamson A., Agüero M., Gonzalez E., Geeves W. 2003. Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27:313–323. DOI: 10.1016/S0308-597X(03)00041-1.
- Beck KG., Zimmerman K., Schardt JD., Stone J., Lukens RR., Reichard S., Randall J., Cangelosi AA., Cooper D., Thompson JP. 2008. Invasive species defined in a policy context: Recommendations from the Federal Invasive Species Advisory Committee. *Invasive Plant Science and Management* 1:414–421. DOI: 10.1614/IPSM-08-089.1.
- Beecher LE., Romaine RP. 2010. Evaluation of baits for harvesting Procambarid

- crawfishes with emphasis on bait type and bait quantity. *Journal of Shellfish Research* 29:13–18. DOI: 10.2983/035.029.0106.
- Behrens Yamada S. 2001. *Global Invader: The European Green Crab*. Corvallis, Oregon: Oregon Sea Grant.
- Behrens Yamada S., Dumbauld BR., Kalin A., Hunt CE., Figlar-Barnes R., Randall A. 2005. Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. *Biological Invasions* 7:309–321. DOI: 10.1007/s10530-004-0877-2.
- Behrens Yamada S., Gillespie GE. 2008. Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? *ICES Journal of Marine Science* 65:725–729. DOI: 10.1093/icesjms/fsm191.
- Behrens Yamada S., Kosro PM. 2010. Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*. *Biological Invasions* 12:1791–1804. DOI: 10.1007/s10530-009-9589-y.
- Bergshoeff JA., McKenzie CH., Best K., Zargarpour N., Favaro B. 2018. Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada. *PeerJ* 6:e4223. DOI: 10.7717/peerj.4223.
- Bergshoeff JA., Zargarpour N., Legge G., Favaro B. 2017. How to build a low-cost underwater camera housing for aquatic research. *FACETS* 2:150–159. DOI:

10.1139/facets-2016-0048.

Berrill M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *Journal of Crustacean Biology* 2:31–39.

Best K., McKenzie CH., Couturier C. 2014. Investigating mitigation of juvenile European green crab *Carcinus maenas* from seed mussels to prevent transfer during Newfoundland mussel aquaculture operations. *Management of Biological Invasions* 5:255–262.

Best K., McKenzie CH., Couturier C. 2017. Reproductive biology of an invasive population of European green crab, *Carcinus maenas*, in Placentia Bay, Newfoundland. *Management of Biological Invasions* 8:247–255.

Beukema JJ. 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *Journal of Experimental Marine Biology and Ecology* 153:97–113. DOI: 10.1016/S0022-0981(05)80009-7.

Blakeslee AMH., Keogh CL., Fowler AE., Griffen BD. 2015. Assessing the effects of trematode infection on invasive green crabs in eastern North America. *PLoS ONE* 10:e0128674. DOI: 10.1371/journal.pone.0128674.

Blakeslee AMH., McKenzie CH., Darling JA., Byers JE., Pringle JM., Roman J. 2010. A hitchhiker's guide to the Maritimes: anthropogenic transport facilitates long-distance dispersal of an invasive marine crab to Newfoundland. *Diversity and Distributions* 16:879–891. DOI: 10.1111/j.1472-4642.2010.00703.x.

- Bolker BM., Brooks ME., Clark CJ., Geange SW., Poulsen JR., Stevens MHH., White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135. DOI: 10.1016/j.tree.2008.10.008.
- Boutson A., Mahasawasde C., Mahasawasde S., Tunkijjanukij S., Arimoto T. 2009. Use of escape vents to improve size and species selectivity of collapsible pot for blue swimming crab *Portunus pelagicus* in Thailand. *Fisheries Science* 75:25–33. DOI: 10.1007/s12562-008-0010-z.
- Broadhurst MK. 2000. Modifications to reduce bycatch in prawn trawls: A review and framework for development. *Reviews in Fish Biology and Fisheries* 10:27–60. DOI: 10.1023/A:1008936820089.
- Broekhuysen GJ. 1936. On development, growth and distribution of *Carcinides maenas* (L.). *Archives Néerlandaises de Zoologie* 2:257–400.
- Butchart SHM., Walpole M., Collen B., Van Strien A., Scharlemann JPW., Almond REA., Baillie JEM., Bomhard B., Brown C., Bruno J., Carpenter KE., Carr GM., Chanson J., Chen R. 2010. Global biodiversity: Indicators of recent declines. *Science* 328:1164–1168. DOI: 10.1126/science.1187512.
- Butt MA. 2017. Bait selection study of the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada. University Centre of the Westfjords Master.
- Cameron B., Metaxas A. 2005. Invasive green crab, *Carcinus maenas*, on the Atlantic

coast and in the Bras d'Or Lakes of Nova Scotia, Canada: Larval supply and recruitment. *Journal of the Marine Biological Association of the United Kingdom* 85:847–855. DOI: 10.1017/S002531540501180X.

Carlton JT., Cohen AN. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography* 30:1809–1820. DOI: 10.1111/j.1365-2699.2003.00962.x.

Clark AS., Jury SH., Goldstein JS., Langley TG. 2017. Underwater video surveillance of American lobsters (*Homarus americanus*) to understand saturation levels in lobster traps. :161–170. DOI: 10.7755/FB.116.2.5.

Cohen AN., Carlton JT., Fountain MC. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology* 122:225–237.

Coutts ADM., Forrest BM. 2007. Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum*. *Journal of Experimental Marine Biology and Ecology* 342:154–162. DOI: 10.1016/j.jembe.2006.10.042.

Crawley MJ. 2012. *The R book*. Chichester, UK: John Wiley & Sons Ltd.

Crisp DJ. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *British Ecological Society* 33:165–210.

- Crothers J. H. 1968. The biology of the shore crab *Carcinus maenas* (L.) 2. The life of the adult crab. *Field Studies* 2:579–614.
- Culver CS., M. Kuris A. 2000. The apparent eradication of a locally established introduced marine pest. *Biological Invasions* 2:245–253. DOI: 10.1023/A:1010082407254.
- Curtis LJF., Curtis DL., Matkin H., Thompson M., Choi F., Callow P., Gillespie GE., Terriault TW., Pearce CM. 2015. Evaluating transfers of harvested shellfish products, from the west to the east coast of Vancouver Island, as a potential vector for European green crab (*Carcinus Maenus*) and other non-indigenous invertebrate species. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2015/014:vi + 74 p.
- Darling JA., Bagley MJ., Roman J., Tepolt CK., Geller JB. 2008. Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. *Molecular Ecology* 17:4992–5007. DOI: 10.1111/j.1365-294X.2008.03978.x.
- DFO. 2011a. Ecological assessment of the invasive European green crab (*Carcinus maenas*) in Newfoundland 2007-2009. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.*:2011/033.
- DFO. 2011b. Proceedings of the Regional Advisory Process on green crab, *Carcinus maenas*, populations and mitigations in the Newfoundland and Labrador region. *DFO Can. Sci. Advis. Sec. Proceed. Ser.* 2011/020.
- DFO. 2016. Oceanographic conditions in the Atlantic zone in 2015. *DFO Can. Sci.*

Advis. Sec. Sci. Advis. Rep.:2016/041.

Duncombe LG., Therriault TW. 2017. Evaluating trapping as a method to control the European green crab, *Carcinus maenas*, population at Pipestem Inlet, British Columbia. *Management of Biological Invasions* 8:235–246.

EPA. 2008. *Effects of climate change on aquatic invasive species and implications for management and research*. Washington, DC: National Center for Environmental Assessment.

Eriksson S., Edlund A-M. 1977. On the ecological energetics of 0-group *Carcinus maenas* (L.) from a shallow sandy bottom in Gullmar Fjord, Sweden. *Journal of Experimental Marine Biology and Ecology* 30:233–248. DOI: [http://dx.doi.org/10.1016/0022-0981\(77\)90033-8](http://dx.doi.org/10.1016/0022-0981(77)90033-8).

Favaro B., Duff SD., Côté IM. 2013. A trap with a twist: evaluating a bycatch reduction device to prevent rockfish capture in crustacean traps. *ICES Journal of Marine Science* 70:114–122.

Favaro B., Duff SD., Côté IM. 2014. Density-dependent catchability of spot prawns (*Pandalus platyceros*) observed using underwater video. *The Journal of Ocean Technology* 9:84–98.

Favaro B., Lichota C., Côté IM., Duff SD. 2012. TrapCam: an inexpensive camera system for studying deep-water animals. *Methods in Ecology and Evolution* 3:39–46. DOI: 10.1111/j.2041-210X.2011.00128.x.

- Furevik DM., Humborstad OB., Jørgensen T., Løkkeborg S. 2008. Floated fish pot eliminates bycatch of red king crab and maintains target catch of cod. *Fisheries Research* 92:23–27. DOI: 10.1016/j.fishres.2007.12.017.
- Furota T., Watanabe S., Watanabe T., Akiyama S., Kinoshita K. 1999. Life history of the Mediterranean green crab, *Carcinus aestuarii* Nardo, in Toyko Bay, Japan. *Crustaceaun Research* 28:5–15.
- Garbary DJ., Miller AG., Williams J., Seymour NR. 2014. Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). *Marine Biology* 161:3–15. DOI: 10.1007/s00227-013-2323-4.
- Gillespie GE., Norgard TC., Anderson ED., Haggarty DR., Phillips AC. 2015. Distribution and biological characteristics of European green crab, *Carcinus maenas*, in British Columbia, 2006-2013. *Canadian Technical Report of Fisheries and Aquatic Sciences* 3120:88p.
- Gillespie GE., Phillips AC., Paltzat DL., Therriault TW. 2007. Status of the European green crab, *Carcinus maenas*, in British Columbia - 2006. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2700:39 p.
- Grant SM., Sullivan R., Hedges KJ. 2018. Greenland shark (*Somniosus microcephalus*) feeding behavior on static fishing gear, effect of SMART (Selective Magnetic and Repellent-Treated) hook deterrent technology, and factors influencing entanglement in bottom longlines. *PeerJ* 6:e4751. DOI: 10.7717/peerj.4751.

- Green SJ., Dulvy NK., Brooks AML., Akins JL., Cooper AB., Miller S., Roté IM. 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* 24:1311–1322. DOI: 10.1890/13-0979.1.
- Grosholz ED., Ruiz GM. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Marine Biology* 122:239–247. DOI: 10.1007/BF00348936.
- Grosholz ED., Ruiz GM. 1996. Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biological Conservation* 78:59–66. DOI: 10.1016/0006-3207(94)00018-2.
- Gurevitch J., Padilla DK. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19:470–474. DOI: 10.1016/j.tree.2004.07.005.
- Hänfling B., Edwards F., Gherardi F. 2011. Invasive alien Crustacea: Dispersal, establishment, impact and control. *BioControl* 56:573–595. DOI: 10.1007/s10526-011-9380-8.
- Hart JFL. 1955. The green crab - a shellfish enemy. Fisheries Research Board of Canada, Report of the Atlantic Biological Station, St. Andrews, N.B. for 1955. :p.11.
- He P. 2003. Swimming behaviour of winter flounder (*Pleuronectes americanus*) on natural fishing grounds as observed by an underwater video camera. *Fisheries Research* 60:507–514. DOI: 10.1016/S0165-7836(02)00086-3.

- Hidalgo FJ., Barón PJ., Orensanz JM. 2005. A prediction come true: The green crab invades the Patagonian coast. *Biological Invasions* 7:547–552. DOI: 10.1007/s10530-004-5452-3.
- Hidalgo FJ., Silliman BR., Bazterrica MC., Bertness MD., Ecolog L De., Biolog D De., Nacional U., Mar D., Bwag CCCC., Plata M., Hall B., Box PO. 2007. Predation on the rocky shores of Patagonia , Argentina. *Estuaries and Coasts* 30:886–894.
- Jeffery NW., Bradbury IR., Stanley RRE., Wringe BF., Van Wyngaarden M., Lowen J Ben., McKenzie CH., Matheson K., Sargent PS., DiBacco C. 2018. Genome-wide evidence of environmentally mediated secondary contact of European green crab (*Carcinus maenas*) lineages in eastern North America. *Evolutionary Applications* 11:869–882. DOI: 10.1111/eva.12601.
- Jeffery NW., DiBacco C., Van Wyngaarden M., Hamilton LC., Stanley RRE., Bernier R., FitzGerald J., Matheson K., McKenzie CH., Nadukkalam Ravindran P., Beiko R., Bradbury IR. 2017. RAD sequencing reveals genomewide divergence between independent invasions of the European green crab (*Carcinus maenas*) in the Northwest Atlantic. *Ecology and Evolution* 7:2513–2524. DOI: 10.1002/ece3.2872.
- Jensen KT., Jensen JN. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 89:157–174. DOI: 10.1016/0022-0981(85)90124-8.

- Jensen GC., McDonald PS., Armstrong DA. 2007. Biotic resistance to green crab, *Carcinus maenas*, in California bays. *Marine Biology* 151:2231–2243. DOI: 10.1007/s00227-007-0658-4.
- Joseph V., Schmidt AL., Gregory RS. 2013. Use of eelgrass habitats by fish in eastern Canada. *Canadian Scientific Advisory Secretariat Science Research Document* 2012/138:ii + 12p.
- Jury SH., Howell H., O’Grady DF., Watson WH., Jury, S.H., Howell, H., O’Grady, D.F.O. & Watson III WH. 2001. Lobster trap video: *in situ* video surveillance of the behaviour of *Homarus americanus* in and around traps. *Marine and Freshwater Research* 52:1125–1132.
- Kahle D., Wickham H. 2013. ggmap: Spatial Visualization with ggplot2. *The R Journal* 5:144–161.
- Kelley AL., de Rivera CE., Grosholz ED., Ruiz GM., Yamada SB., Gillespie G. 2015. Thermogeographic variation in body size of *Carcinus maenas*, the European green crab. *Marine Biology* 162:1625–1635. DOI: 10.1007/s00227-015-2698-5.
- Kersey Sturdivant S., Clark KL. 2011. An evaluation of the effects of blue crab (*Callinectes sapidus*) behavior on the efficacy of crab pots as a tool for estimating population abundance. *Fishery Bulletin* 109:48–55.
- Kimbrow DL., Grosholz ED., Baukus AJ., Nesbitt NJ., Travis NM., Attie S., Coleman-Hulbert C. 2009. Invasive species cause large-scale loss of native California oyster

- habitat by disrupting trophic cascades. *Oecologia* 160:563–575. DOI: 10.1007/s00442-009-1322-0.
- Klassen G., Locke A. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2818:1–82.
- Lehnert SJ., Dibacco C., Jeffery NW., April MH., Isaksson J., Roman J., Wringe BF., Ryan RE., Matheson K., Mckenzie CH., Hamilton LC., Bradbury R. 2018. Temporal dynamics of the genetic clines of invasive European green crab (*Carcinus maenas*) in eastern North America. *Evolutionary Applications* Accepted. DOI: 10.1111/eva.12657.
- Leignel V., Stillman JH., Baringou S., Thabet R., Metais I. 2014. Overview on the European green crab *Carcinus* spp. (Portunidae, Decapoda), one of the most famous marine invaders and ecotoxicological models. *Environmental Science and Pollution Research* 21:9129–9144. DOI: 10.1007/s11356-014-2979-4.
- Leim AH. 1951. Unusual marine species on the Atlantic coast in 1951. In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1951. :138–140.
- Ljungberg P., Lunneryd SG., Lövgren J., Königson S. 2016. Including cod (*Gadus morhua*) behavioural analysis to evaluate entrance type dependent pot catch in the Baltic sea. *Journal of Ocean Technology* 11:48–63.
- Lodge DM., Williams S., MacIsaac HJ., Hayes KR., Leung B., Reichard S., Mack RN.,

- Moyle PB., Smith M., Andow DA., Carlton JT., McMichael A. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16:2035–2054. DOI: 10.1890/04-0922.
- Lowe S., Browne M., Boudjelas S., De Poorter M. 2000. *100 of the world's worst invasive alien species: a selection from the global invasive species database*. Invasive Species Specialist group (ISSG), specialist group of the Species Survival Commission (SSC) of the World, Conservation Union (IUCN).
- MacPhail JS. 1953. Abundance and distribution of the green crab – a clam predator. In: Needler, A.W.H. Fisheries Research Board of Canada, Report of the Atlantic Biological Station for 1953. :33–34.
- Malyshev A., Quijón PA. 2011. Disruption of essential habitat by a coastal invader: New evidence of the effects of green crabs on eelgrass beds. *ICES Journal of Marine Science* 68:1852–1856. DOI: 10.1093/icesjms/fsr126.
- Matheson K., Gagnon P. 2012. Temperature mediates non-competitive foraging in indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs from Newfoundland and Labrador. *Journal of Experimental Marine Biology and Ecology* 414–415:6–18. DOI: 10.1016/j.jembe.2012.01.006.
- Matheson K., McKenzie CH. 2014. Predation of sea scallops and other indigenous bivalves by invasive green crab, *Carcinus maenas*, from Newfoundland, Canada. *Journal of Shellfish Research* 33:495–501. DOI: 10.2983/035.033.0218.

- Matheson K., McKenzie CH., Gregory RS., Robichaud DA., Bradbury IR., Snelgrove PVR., Rose GA. 2016. Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. *Marine Ecology Progress Series* 548:31–45. DOI: 10.3354/meps11674.
- McKenzie CH., Han G., He M., Wells T., Maillet G. 2011. Alternate ballast water exchange zones for the Newfoundland and Labrador region – an aquatic invasive species risk assessment based on oceanographic modelling, ecologically and biologically significant areas and the sustainability of fisheries and aquacul. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2010/087:viii + 39 p.
- McNive MA., Quijon PA., Mitchell AW. 2013. Composition and distribution of the European green crab in Prince Edward Island, Canada. *Journal of Animal Science* 3:295–298.
- Meintzer P., Walsh P., Favaro B. 2017. Will you swim into my parlour? *In situ* observations of Atlantic cod (*Gadus morhua*) interactions with baited pots, with implications for gear design. *PeerJ* 5:e2953. DOI: 10.7717/peerj.2953.
- Meintzer P., Walsh P., Favaro B. 2018. Comparing catch efficiency of five models of pot for use in a Newfoundland and Labrador cod fishery. *PLOS ONE* 13:1–18. DOI: 10.1371/journal.pone.0199702.
- Miller RJ. 1978. Entry of *Cancer productusto* to baited traps. *ICES Journal of Marine Science* 38:220–225. DOI: 10.1093/icesjms/38.2.220.

- Miller RJ. 1979. Saturation of crab traps: Reduced entry and escapement. *ICES Journal of Marine Science* 38:338–345. DOI: 10.1093/icesjms/38.3.338.
- Miller RJ. 1990. Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1228–1251. DOI: 10.1139/f90-143.
- Miller RJ., Rodger RS. 1996. Soak times and fishing strategy for American lobster. *Fisheries Research* 26:199–205. DOI: 10.1016/0165-7836(95)00445-9.
- Miron G., Audet D., Landry T., Moriyasu M. 2005. Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. *Journal of Shellfish Research* 24:579–586. DOI: 10.2983/0730-8000(2005)24.
- Molnar JL., Gamboa RL., Revenga C., Spalding MD. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6:485–492. DOI: 10.1890/070064.
- Moran M., Jenke J. 1990. Effects of fish trap mesh size on species and size selectivity in the Australian North West Shelf trap fishery. *Fishbyte* 8:8–13.
- Murray LG., Seed R. 2010. Determining whether catch per unit effort is a suitable proxy for relative crab abundance. *Marine Ecology Progress Series* 401:173–182. DOI: 10.3354/meps08415.
- Myers JH., Simberloff D., Kuris AM., Carey JR. 2000. Eradication revisited: Dealing

- with exotic species. *Trends in Ecology and Evolution* 15:316–320. DOI: 10.1016/S0169-5347(00)01914-5.
- Nguyen TX., Winger PD., Legge G., Dawe EG., Mullooney DR. 2014. Underwater observations of the behaviour of snow crab (*Chionoecetes opilio*) encountering a shrimp trawl off northeast Newfoundland. *Fisheries Research* 156:9–13. DOI: 10.1016/j.fishres.2014.04.013.
- Nguyen KQ., Winger PD., Morris C., Grant SM. 2017. Artificial lights improve the catchability of snow crab (*Chionoecetes opilio*) traps. *Aquaculture and Fisheries* 2:124–133. DOI: 10.1016/j.aaf.2017.05.001.
- Orth RJ., Carruthers TJB., Dennison WC., Duarte CM., Fourqurean JW., Heck KL., Hughes AR., Kendrick GA., Kenworthy WJ., Olyarnik S., Short FT., Waycott M., Williams SL. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56:987–996. DOI: 10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2.
- Ovegård M., Königson S., Persson A., Lunneryd SG. 2011. Size selective capture of Atlantic cod (*Gadus morhua*) in floating pots. *Fisheries Research* 107:239–244. DOI: 10.1016/j.fishres.2010.10.023.
- Pasko S., Goldberg J. 2014. Review of harvest incentives to control invasive species. *Management of Biological Invasions* 5:263–277. DOI: 10.3391/mbi.2014.5.3.10.
- Perrings C. 2005. Mitigation and adaptation strategies for the control of biological invasions. *Ecological Economics* 52:315–325. DOI:

10.1016/j.ecolecon.2004.08.001.

Pickering T., Quijón PA. 2011. Potential effects of a non-indigenous predator in its expanded range: Assessing green crab, *Carcinus maenas*, prey preference in a productive coastal area of Atlantic Canada. *Marine Biology* 158:2065–2078. DOI: 10.1007/s00227-011-1713-8.

Pinhero J., Bates D., Debroy S., Sarkar D., R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1-131, <https://cran.r-project.org/package=nlme>.

Pintor LM., Sih A., Bauer ML., Pintor LM., Sih A., Bauer ML. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos* 117:1629–1636.

Poirier LA., Tang S., Mohan J., O'Connor E., Dennis E., Abdullah M., Zhou D., Stryhn H., St-Hilaire S., Quijón PA. 2018. A novel bycatch reduction device (BRD) and its use in a directed fishery for non-indigenous green crabs (*C. maenas*) in Atlantic Canada. *Fisheries Research* 204:165–171. DOI: 10.1016/j.fishres.2018.02.018.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

Rehage JS., Sih A. 2004. Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. *Biological Invasions* 6:379–391. DOI:

10.1023/B:BINV.0000034618.93140.a5.

Reid DG., Naylor E. 1994. Size-related mating success in the shore crab *Carcinus maenas* (Crustacea: Brachyura). *Journal of Zoology, London* 232:397–407.

Robbins WD., Peddemors VM., Broadhurst MK., Gray CA. 2013. Hooked on fishing? Recreational angling interactions with the Critically Endangered grey nurse shark *Carcharias taurus* in eastern Australia. *Endangered Species Research* 21:161–170. DOI: 10.3354/esr00520.

Robinson TB., Griffiths CL., Kruger N. 2004. Distribution and status of marine invasive species in and bordering the West Coast National Park. *Koedoe* 47:79–87. DOI: 10.4102/koedoe.v47i1.73.

Roman J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences* 273:2453–2459. DOI: 10.1098/rspb.2006.3597.

Roman J., Palumbi SR. 2004. A global invader at home: Population structure of the green crab, *Carcinus maenas*, in Europe. *Molecular Ecology* 13:2891–2898. DOI: 10.1111/j.1365-294X.2004.02255.x.

Ropes JW. 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). *Fishery Bulletin* 67:183–203.

Rossong MA., Quijón PA., Snelgrove PVR., Barrett TJ., McKenzie CH., Locke A. 2012.

- Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada. *Biological Invasions* 14:659–669. DOI: 10.1007/s10530-011-0107-7.
- Rossong MA., Williams PJ., Comeau M., Mitchell SC., Apaloo J. 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). *Journal of Experimental Marine Biology and Ecology* 329:281–288. DOI: 10.1016/j.jembe.2005.09.007.
- Le Roux PJ., Branch GM., Joska MAP. 1990. On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. *South African Journal of Marine Science* 9:85–93. DOI: 10.2989/025776190784378835.
- Say T. 1817. An account of the crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 1:57–63.
- Secord D. 2003. Biological control of marine invasive species: cautionary tales and land-base lessons. *Biological Invasions* 5:117–131. DOI: 10.1023/A:1024054909052.
- Serena M., Grant TR., Williams GA. 2016. Reducing bycatch mortality in crustacean traps: Effect of trap design on platypus and yabby retention rates. *Fisheries Research* 175:43–50. DOI: 10.1016/j.fishres.2015.11.010.
- Sheaves MJ. 1995. Effects of design modifications and soak time variations on Antillean-

- z fish trap performance in a tropical estuary. *Bulletin of Marine Science* 56:475–489.
- Shelton RGJ., Mackie AM. 1971. Studies on the chemical preferences of the shore crab, *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 7:41–49. DOI: 10.1016/0022-0981(71)90003-7.
- Simberloff D. 2001. Eradication of island invasives: practical actions and results achieved. *Trends in Ecology and Evolution* 16:273–274. DOI: 10.1016/S0169-5347(01)02154-1.
- Smith LD. 2004. Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. *Marine Ecology Progress Series* 276:209–222. DOI: 10.3354/meps276209.
- Souza AT., Ilarri MI., Campos J., Marques JC., Martins I. 2011. Differences in the neighborhood: Structural variations in the carapace of shore crabs *Carcinus maenas* (Decapoda: Portunidae). *Estuarine, Coastal and Shelf Science* 95:424–430. DOI: 10.1016/j.ecss.2011.06.021.
- St-Hilaire S., Krause J., Wight K., Poirier L., Singh K. 2016. Break-even analysis for a green crab fishery in PEI, Canada. *Management of Biological Invasions* 7:297–303. DOI: 10.3391/mbi.2016.7.3.09.
- Styrishave B., Rewitz K., Andersen O. 2004. Frequency of moulting by shore crabs *Carcinus maenas* (L.) changes their colour and their success in mating and physiological performance. *Journal of Experimental Marine Biology and Ecology*

313:317–336. DOI: 10.1016/j.jembe.2004.08.013.

- Suuronen P., Chopin F., Glass C., Løkkeborg S., Matsushita Y., Queirolo D., Rihan D. 2012. Low impact and fuel efficient fishing-Looking beyond the horizon. *Fisheries Research* 119–120:135–146. DOI: 10.1016/j.fishres.2011.12.009.
- Taylor CM., Hastings A. 2004. Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *Journal of Applied Ecology* 41:1049–1057. DOI: 10.1111/j.0021-8901.2004.00979.x.
- Therriault TW., Herborg L., Locke A., Mckindsey CW. 2008. Risk assessment for European green crab (*Carcinus maenas*) and Chinese mitten crab (*Eriocheir sinensis*) in Canadian waters. *Canadian Science Advisory Secretariat*:40.
- Thresher RE., Kuris AM. 2004. Options for managing invasive marine species. *Biological Invasions* 6:295–300. DOI: 10.1023/B:BINV.0000034598.28718.2e.
- Thresher R., Proctor C., Ruiz GM., Gurney R., MacKinnon C., Walton WC., Rodriguez L., Bax N. 2003. Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. *Marine Biology* 142:867–876. DOI: 10.1007/s00227-003-1011-1.
- Thresher RE., Werner M., Høeg JT., Svane I., Glenner H., Murphy NE., Wittwer C. 2000. Developing the options for managing marine pests: Specificity trials on the parasitic castrator, *Sacculina carcini*, against the European crab, *Carcinus maenas*, and related species. *Journal of Experimental Marine Biology and Ecology* 254:37–51. DOI: 10.1016/S0022-0981(00)00260-4.

Underwood MJ., Winger PD., Fernö A., Engås A. 2015. Behavior-dependent selectivity of yellowtail flounder (*Limanda ferruginea*) in the mouth of a commercial bottom trawl. *Fishery Bulletin* 113:430–441. DOI: 10.7755/FB.113.6.

Underwood M., Winger PD., Legge G. 2012. Development and evaluation of a new high definition self-contained underwater camera system to observe fish and fishing gears in situ. *The Journal of Ocean Technology* 7:59–70.

Vazquez Archdale M., Anasco CP., Nakagawa A. 2010. Liftnets compare favorably with pots as harvesting fishing gear for invasive swimming crabs. *Journal of Fisheries and Aquatic Science* 5:510–516.

Vazquez Archdale M., Anraku K., Yamamoto T., Higashitani N. 2003. Behavior of the Japanese rock crab “Ishigani” *Charybdis japonica* towards two collapsible baited pots: Evaluation of capture effectiveness. *Fisheries Science* 69:785–791. DOI: 10.1046/j.1444-2906.2003.00687.x.

Vazquez Archdale M., Kawamura G. 2011. Evaluation of artificial and natural baits for the pot fishery of the sand crab *Ovalipes punctatus* (De Haan, 1833). *Fisheries Research* 111:159–163. DOI: 10.1016/j.fishres.2011.07.006.

Vercaemer B., Sephton D. 2016. European green crab (*Carcinus maenas*) monitoring in the Maritimes Region 2008-2015. *Can. Tech. Rep. Fish. Aquat. Sci.* 3147:v + 56p.

Walton WC., MacKinnon C., Rodriguez LF., Proctor C., Ruiz GM. 2002. Effect of an invasive crab upon a marine fishery: Green crab, *Carcinus maenas*, predation upon a

- venerid clam, *Katelysia scalarina*, in Tasmania (Australia). *Journal of Experimental Marine Biology and Ecology* 272:171–189. DOI: 10.1016/S0022-0981(02)00127-2.
- Watson W., Jury SH. 2013. The relationship between American lobster catch, entry rate into traps and density. *Marine Biology Research* 9:59–68. DOI: 10.1080/17451000.2012.727430.
- Weis JS. 2010. The role of behavior in the success of invasive crustaceans. *Marine and Freshwater Behaviour and Physiology* 43:83–98. DOI: 10.1080/10236244.2010.480838.
- Welch WR. 1968. Changes in abundance of green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. *United States Fish and Wildlife Service Fishery Bulletin* 67:337–345.
- Williams AB. 1984. *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Washington, DC: Smithsonian Institution Press.
- Williams K., De Robertis A., Berkowitz Z., Rooper C., Towler R. 2014. An underwater stereo-camera trap. *Methods in Oceanography* 11:1–12. DOI: 10.1016/j.mio.2015.01.003.
- Winger PD., Walsh PJ. 2011. Selectivity, efficiency, and underwater observations of modified trap designs for the snow crab (*Chionoecetes opilio*) fishery in Newfoundland and Labrador. *Fisheries Research* 109:107–113. DOI: 10.1016/j.fishres.2011.01.025.

- Woll AK., Boje J., Holst R., Gundersen AC. 2001. Catch rates and hook and bait selectivity in longline fishery for Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) at East Greenland. *Fisheries Research* 51:237–246. DOI: 10.1016/S0165-7836(01)00249-1.
- Zhou S., Shirley TC. 1997. Performance of two red king crab pot designs. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1858–1864. DOI: 10.1139/cjfas-54-8-1858.
- Zuur AF., Ieno EN. 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution* 7:636–645. DOI: 10.1111/2041-210X.12577.